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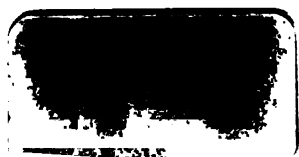
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VOLUME XVIII

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CONTENTS OF VOLUME XVIII, 1908

Number 1, January, 1908.

An Experimental Study of Imitation in Cats. By CHARLES SCOTT BERRY. (<i>From the Harvard Psychological Laboratory.</i>) With Two Figures	1
Orientation in the White Rat. By HARVEY CARR and JOHN B. WATSON. (<i>From the Psychological Laboratory of the University of Chicago.</i>) With One Figure.....	27
Studies on Nerve Cells. I. The Molluscan Nerve Cell, Together with Summaries of Recent Literature on the Cytology of Invertebrate Nerve Cells. By W. M. SMALLWOOD and CHARLES G. ROGERS. (<i>From the Zoological Laboratory of Syracuse University.</i>) With Plate I and Thirteen Figures in the Text.....	45
Document I of the Report of the President of the Brain Commission (Br. C.). By W. WALDEYER. Neurology at the Physiological Congress, Heidelberg, 1907. and at the Congress for Psychiatry, Neurology, Psychology and the Nursing of the Insane, Amsterdam, September, 1907. By SHEPHERD IVORY FRANZ.....	87
Books Received	91
	100

Number 2, April, 1908.

The Architectural Relations of the Afferent Elements Entering into the Formation of the Spinal Nerves. By S. WALTER RANSON, (<i>From the Anatomical Laboratory of the University of Chicago.</i>) With One Figure.....	101
The Nervous System of the American Leopard Frog, <i>Rana pipiens</i> , Compared with that of the European Frogs, <i>Rana esculenta</i> <i>Rana temporaria</i> (<i>fusca</i>). By HENRY H. DONALDSON. (<i>From the Wistar Institute of Anatomy and Biology.</i>) With Six Figures.....	121
Preliminary Note on the Size and Condition of the Central Nervous System in Albino Rats Experimentally Stunted. By SHINKISHI HATAI. (<i>From the Wistar Institute of Anatomy and Biology</i>).....	151
On the Phylogenetic Differentiation of the Organs of Smell and Taste—By C. JUDSON HERRICK. (<i>From the Anatomical Laboratory of the University of Chicago</i>).....	157
Some Conditions which Determine the Length of the Internodes found on the Nerve Fibers of the Leopard Frog, <i>Rana pipiens</i> . By KATASHI TAKAHASHI. (<i>From the Neurological Laboratory of the University of Chicago.</i>) With Seven Figures.....	167

Number 3, June, 1908.

The Behavior of the Larval and Adolescent Stages of the American Lobster (<i>Homarus Americanus</i>) By PHILIP B. HADLEY. (<i>From the Anatomical Laboratory of Brown University.</i>) With Twenty-two Figures.....	199
The Reactions to Light of the Decapitated Young <i>Necturus</i> . By A. C. EYLESHTYMER. (<i>From the Anatomical Laboratory of St. Louis University.</i>).....	303
Recent Studies upon the Locomotor Responses of Animals to White Light. By E. D. CONGDON...	309
Literary Notices.....	329

Number 4, October, 1908.

A Comparison of the Albino Rat with Man in Respect to the Growth of the Brain and of the Spinal Cord. By HENRY H. DONALDSON. (<i>From the Wistar Institute of Anatomy.</i>) With Plates II and III and One Figure in the Text.....	345
The Morphological Subdivision of the Brain. By C. JUDSON HERRICK. (<i>From the Anatomical Laboratory of the University of Chicago.</i>).....	393
On the Commissura Infima and its Nuclei in the Brains of Fishes. By C. JUDSON HERRICK. (<i>From the Anatomical Laboratory of the University of Chicago.</i>) With Twelve Figures.....	409
Eversion and Inversion of the Dorsal-Lateral Wall in Different Parts of the Brain. By C. U. ARJENS KAPPERS. (<i>Central Institute for Brain Research, Amsterdam.</i>) With Five Figures.	433

Number 5, November, 1908.

The Relations of Comparative Anatomy to Comparative Psychology. LUDWIG EDINGER. (<i>From the Senckenberg Neurological Institute, Frankfurt a /M.</i>) With Five Figures.....	437
The Relation of Strength of Stimulus to Rapidity of Habit Formation. By ROBERT M. YERKES and JOHN D. DODSON. (<i>From the Harvard Psychological Laboratory.</i>) With Five Figures	459
Some Reactions of <i>Drosophila</i> , with Special Reference to Convulsive Reflexes. By FREDERIC W. CARPENTER. (<i>From the Zoological Laboratory of the University of Illinois.</i>) With One Figure.....	483
Phototaxis in Fiddler Crabs and its Relation to Theories of Orientation. By S. J. HOLMES. (<i>From the Zoological Laboratory of the University of Wisconsin</i>)	493
The Limits of Educability in <i>Paramecium</i> . By STEVENSON SMITH. (<i>From Hampden-Sidney Col- lege, Virginia.</i>) With Four Figures.....	499
French Work in Comparative Psychology for the Past Two Years. By MARGARET FLOY WASH- BURN. (<i>From the Department of Psychology of Vassar College.</i>).....	511
Literary Notices	521

[Number 6, December, 1908.

The Cranial Nerves of <i>Amphiuma</i> means. By H. W. NORRIS. (<i>Iowa College.</i>) With Plates IV, V, VI, VII and VIII.....	527
Additional Notes on the Cranial Nerves of <i>Petromyzonts</i> . By J. B. JOHNSTON. (<i>University of Minnesota.</i>) With Thirty-one Figures	569
On the Significance of the Caliber of the Parts of the Neurone in Vertebrates. By J. B. JOHNSTON. (<i>University of Minnesota</i>)	609
Aberrant Roots and Branches of the Abducent and Hypoglossal Nerves. By JOHN LEWIS BREMER. (<i>Histological Laboratory, Harvard Medical School.</i>) With Nine Figures.....	619
The Commissures and the Neurocord Cells of the Brain of <i>Cerebratulus lacteus</i> . By CAROLINE BURLING THOMPSON. (<i>Wellesley College.</i>) With Thirteen Figures	641
Editorial. Two Recent Tendencies in Cerebral Morphology.....	663

SUBJECT AND AUTHOR INDEX.

VOLUME XVIII.

Authors' names are in small caps. References to subjects and authors of original articles are marked with an asterisk.

- A**BDUCENT nerve, aberrant roots and branches of, 619.
 Aberrant roots and branches of the abducent and hypoglossal nerves, 619.
 Adolescent stages in American lobster, 199.
 Afferent elements entering into the formation of the spinal nerves, Architectural relations of the, 101.
 American Journal of Psychology, 339.
 Amphiuma, cranial nerves of, 527.
 *ANGIER, ROSWELL P. Review of Franz's functions of the cerebrum, 333.
 Anatomy, comparative, relations to comparative psychology, 437.
 Animal behavior, the dancing mouse, 336.
 Animal intelligence, a study in, 339.
 Ant, carpenter, life history of, 521.
 Architectural relations of the afferent elements entering into the formation of the spinal nerves, 101.
- B**EES, as reflex machines, 524.
 Behavior, animal, the dancing mouse, 336.
 of the larval and adolescent stages of the American lobster, 199.
 of star fish, 523.
 *BERRY, CHARLES SCOTT, An experimental study of imitation in cats, 1.
 Biological Bulletin, 521.
 Brain, of Cerebratulus, commissures and neurocord cells in, 641.
 Commission. Document I, of the report of the President of the, 87.
 eversion and inversion of the Dorso-Lateral wall in different parts of the, 433.
 of fishes, commissura infima and its nuclei in the, 409.
 growth of, in the albino rat, 345.
 morphological subdivision of, 393.
 *BREMER, JOHN LEWIS. Aberrant roots and branches of the abducent and hypoglossal nerves, 619.
- BUTTEL-REEPEN, H. V. Are bees reflex machines? An experimental contribution to the natural history of the honey bee, 524.
- C**ALIBER of parts of the neurone in vertebrates, 601.
 *CARPENTER, FREDERICK W. Some reactions of *Drosophila* with Special reference to convulsive reflexes, 483.
 *CARR, HARVEY, with JOHN B. WATSON. Orientation in the white rat, 27.
 Cats, experimental study of imitation in, 1.
 Cerebral morphology, two recent tendencies in, 663.
 Cerebratulus, commissures and neurocord cells in brain of, 641.
 Cerebrum, the functions of, 333.
 Children, psychology of mentally deficient, 332.
 COLE, LEON J. An experimental study of the image forming powers of various types of eyes, 525.
 *COLE, L. W., Review of Davis's the raccoon, 339.
 Review of Jennings' behavior of the starfish, 529.
 Commissura infima and its nuclei in the brain of fishes, 409.
 Commissures and the neurocord cells of the brain of Cerebratulus, 641.
 Comparative anatomy, relations to comparative psychology, 437.
 Comparative psychology, relations of comparative anatomy to, 437.
 Comparison of the albino rat with man in respect to the growth of the brain and of the spinal cord, 345.
 *CONGDON, E. D. Recent studies upon the locomotor responses of animals to white light, 309.
 Congress, neurology at the physiological, Heidelberg, 1907, 91.
 neurology at the, for psychiatry, neurology, psychology and the nursing of the insane, Amsterdam, September, 1907, 91.
 Convulsive reflexes in *Drosophila*, 483.
 Cranial nerves of amphiuma means, 527.
 of Petromyzonts, 569.

DAVIS, H. B. Study in animal intelligence, 339.
Decapitated, reactions to light of the young, *necturus*, 303.

Differentiation, phylogenetic, of the organs of smell and taste, 157.

Divisions of the brain, morphological, 393.

*DODSON, JOHN D., with ROBERT M. YERKES. Relation of the strength of stimulus to the rapidity of habit formation, 459.

*DONALDSON, H. H., comparison of the albino rat with man in respect to the growth of the brain and of the spinal cord, 345.

*The nervous system of the American leopard frog, *Rana pipiens*, compared with that of the European frogs, *Rana esculenta* and *Rana temporaria* (*fusca*), 121.

Drosophila, reactions of, 483.

*E DINGER, LUDWIG. Relations of comparative anatomy to comparative psychology, 437.

Educability, limits of, in *Paramoecium*, 499.

Eversion and inversion of the dorso-lateral wall in different parts of the brain, 433.

Experimental animal and human psychology, 329.

Experimental study of imitation in cats, 1.

*EYCLESHYMER, A. C. The reactions of light of the decapitated young *necturus*, 303.

Eyes, image-forming powers of various types of, 525.

FIDDLER crabs, phototaxis in, 493.

FRANZ, SHEPHERD IVORY. The functions of the cerebrum: The frontal lobes, 333.

Neurology at the physiological congress, Heidelberg, 1907, and at the congress of psychiatry, neurology, psychology and the nursing of the insane, Amsterdam, September, 1907, 91.

French work in comparative psychology for the past two years, 511.

Frogs, nervous system of American and European, 121.

Frontal lobes, the functions of the cerebrum, 333.

Functions of the cerebrum, the frontal lobes, 333.

GROWTH of the brain and spinal cord in the albino rat, 345.

HABIT formation, relation of the strength of stimulus to rapidity of, 459.

*HADLEY, PHILIP B. The behavior of the larval and adolescent stages of the American lobster, 199.

*HATAI, SHINKISHI. Preliminary note on the size and condition of the central nervous system in albino rats experimentally stunted, 151.

*HERRICK, C. JUDSON. Commissura infima and its nuclei in the brain of fishes, 409.

*Morphological divisions of the brain, 393.

*On the phylogenetic differentiation of the organs of smell and taste, 157.

*Two recent tendencies in cerebral morphology, 663.

*HOLMES, S. J. Phototaxis in fiddler crabs and its relation to theories of orientation, 493.

*HOLT, EDWIN B. Review of Buttell-Reepen's *Are bees reflex machines*, 524.

*Review of Cole's experimental study of the image-forming powers of various types of eyes, 525.

*Review of Yale psychological studies, 331.

Horse, the, of Herr von Osten (*Der kluge Hans*), 329.

Hypoglossal nerve, aberrant roots and branches of, 619.

IIMAGE-FORMING powers of various types of eyes, 525.

Imitation, experimental study of, in cats, 1.

Influence of bodily posture on mental activities, 335.

Intelligence, animal, 339.

Internodes, length of the, on nerve fibers of leopard frog, *Rana pipiens*, 167.

Inversion of the dorso-lateral wall in different parts of the brain, eversion and, 433.

Invertebrate, cytology of, nerve cells, 45.

JENNINGS, H. S. Behavior of the star fish *Asterias forsteri* de Lorient, 523.

*JOHNSTON, J. B. Additional notes on the cranial nerves of *Petromyzonts*, 569.

*Significance of the caliber of the parts of the neurone in vertebrates, 601.

JONES, E. E. Influence of bodily posture on mental activities, 335.

JUDD, CHARLES H. *Yale Psychological Studies*, 331.

*K APPERS, C. U. A. Eversion and inversion of the dorso-lateral wall in different parts of the brain, 433.

LAPISKY, ABRAM. Rhythm as a distinguishing characteristic of prose style, 335.

Larval stages in American lobster, 199.

Light, white, locomotor responses of animals to, 309.
reactions to, of the decapitated young *necturus*, 303.

Limits of educability, in *Paramoecium*, 499.

Literary merit, statistical study of, 336.

Literature, recent, on the Cytology of invertebrate nerve cells, 45.

Lobster, American, behavior of the larval and adolescent stages of, 199.

Locomotor responses of animals to white light, 309.

MEASUREMENT, empirical studies on the theories of, 335.

Mental activities, influence of bodily posture on, 335.

Molluscan nerve cell, 45.

Morphological subdivisions of the brain, 393.

NECTURUS, reactions to light of the decapitated young, 303.

Neurocord cells of the brain of *Cerebratulus*, 64.

Neurology, at the physiological congress, Heidelberg, 1907, 91.

at the congress for psychiatry, neurology, psychology and the nursing of the insane, Amsterdam, 1907, 91.

Neurone, caliber of the, in vertebrates, 601.

Nerve cells, studies on, I. The molluscan nerve cell, together with summaries of recent literature on the cytology of invertebrate nerve cells, 45.

Nerve fibers, length of the internodes on the, of leopard frog, *Rana pipiens*, 167.

Nerves, abducent and hypoglossal, aberrant roots and branches of, 619.

cranial, of amphiuma means, 527.

cranial, of petromyzons, 569.

Nervous system, central, size and condition of the, in albino rats, experimentally stunted, 151.
of the American leopard frog—European frogs, 121.

*NORRIS, H. W. Cranial nerves of amphiuma means, 527.

NORSWORTHY, NAOMI. Psychology of mentally deficient children, 332.

Nuclei, of the commissura infima in the brain of fishes, 409.

ORIENTATION, phototaxis in fiddler crabs and its relation to theories of, 493.

Orientation in the white rat, 27.

PARAMOECIUM, limits of educability in, 499.
Petromyzons, cranial nerves of, 569.

PFUNGST, OSKAR. Das Pferd des Herrn von Osten (Der kluge Hans), 329.

Phototaxis in fiddler crabs, 493.

Phylogenetic differentiation of the organs of smell and taste, 157.

PRICER, JNO. L. The life history of the carpenter ant, 521.

Proceedings American Academy of Arts and Sciences, 525.

Psychology, archives of, 332, 333, 335, 336.

Psychology, comparative, relations of comparative anatomy to, 437.

Psychology, comparative, French work in, for the past two years, 511.

Psychology, human and animal, 329.

of mentally deficient children, 332.

Psychological studies, Yale, 331.

RANA, nervous system of, 121.

RANSON, S. WALTER. The architectural relations of the afferent elements entering into the formation of the spinal nerves, 101.

Rat, comparison of the albino, with men in respect to the growth of the brain and spinal cord, 345.

orientation in the white, 27.

Rats, size and condition of central nervous system in albino, experimentally stunted, 151.

Reactions of *Drosophila* with special reference to convulsive reflexes, 483.

Reactions to light of the decapitated young *necturus*, 303.

Reflexes, convulsive, reaction of *Drosophila* with special reference to, 483.

Relation of the strength of stimulus to the rapidity of habit formation, 459.

Relations of comparative anatomy to comparative psychology, 437.

Responses, locomotor, of animals to white light, 309.

*ROGERS, CHARLES G., with W. M. SMALLWOOD. Studies on nerve cells. I. The molluscan nerve cell, together with summaries of recent literature, on the cytology of invertebrate nerve cells, 45.

Roots, aberrant, and branches of abducent and hypoglossal nerves, 619.

RUEDIGER, W. C. Field of distinct vision, with especial reference to individual differences and their correlations, 335.

SIGNIFICANCE of the caliber of the parts of the neurone in vertebrates, 601.

*SMALLWOOD, W. M., with CHARLES G. ROGERS. Studies on nerve cells. I. The molluscan nerve cell, together with summaries of recent literature on the cytology of invertebrate nerve cells, 25.

Smell, phylogenetic differentiation of the organ of, and taste, 157.

*SMITH, STEVENSON. Limits of educability in *Paramoecium*, 499.

Spinal cord, growth of, in the albino rat, 345.

Spinal nerves, architectural relations of the afferent elements entering into the formation of the, 101.

Star fish, behavior of, 523.

Stimulus, relation of the strength of, to the rapidity of habit formation, 459.

STUMPF, PROF. C., 329.

Stunted size and condition of the central nervous system in albino rats, experimentally, 151.

Subdivisions of the brain, morphological, 393.

*TAKAHASHI, KATASHI. Some conditions which determine the length of the internodes found on the nerve fibers of the leopard frog, *Rana pipiens*, 167.

Taste, phylogenetic differentiation of the organ of smell and, 157.

Tendencies in cerebral morphology, two recent, 663.

Theory of measurement, 335.

*THOMPSON, CAROLINE BURLING. Commissures and the neurocord cells of the brain of *Cerebratulus*, 641.

THORNDIKE, EDWARD L. Empirical studies on the theory of measurement, 335.

*TURNER, C. H. Review of Pricer's life history of the carpenter ant, 523.

Two recent tendencies in cerebral morphology, 663.

UNIVERSITY OF CALIFORNIA publications, 523.

VERTEBRATES, caliber of the neurones in, 601.
Vision, Field of distinct, 335.

*WALDEYER, W. Document I of the report of the President of the Brain Commission, 87.

*WASHBURN, MARGARET F. Review of Yerkes's The dancing mouse, 339.

*French work in comparative psychology for the past two years, 511.

*WATSON, JOHN B., with HARVEY CARR. Orientation in the white rat, 27.

*Review of Pfungst's Das Pferd des Herrn von Osten, 329.

WELLS, F. L. Statistical study of literary merit with remarks on some new phases of the method 336.

WOODWORTH, R. S. Archives of psychology, 332.

YERKES, ROBERT M. The dancing mouse, 336.
*Review of Norsworthy's psychology of mentally deficient children, 332.

*YERKES, ROBERT M., with JOHN D. DODSON. Relation of the strength of stimulus to rapidity of habit formation, 459.
Yale psychological studies, 331.

The Journal of Comparative Neurology and Psychology

VOLUME XVIII

JANUARY, 1908

NUMBER I

AN EXPERIMENTAL STUDY OF IMITATION IN CATS.¹

BY

CHARLES SCOTT BERRY

(*From the Harvard Psychological Laboratory.*)

WITH TWO FIGURES.

I. PROBLEM AND METHOD.....	I
II. EXPERIMENTS:	
1. Jumping from Box to Table.....	2
2. Opening Door by Pulling Knot.....	2
3. Opening Door by Turning Button and Pulling Loop.....	6
4. Getting Food by Turning Button.....	9
5. Raising Small Trap-door.....	10
6. Rolling Ball into Hole.....	11
7. Learning to Catch Mice.....	15
8. Getting Meat out of Bottle.....	18
9. Getting Down from Top of Cage.....	19
III. DISCUSSION OF RESULTS.....	19

I. PROBLEM AND METHOD.

This paper gives an account of some experiments which were made for the purpose of determining to what extent imitation is a factor in the development of the cat. It is a continuation of the study of imitation which was begun with the white rat.²

The experiments now to be described were made with four Manx cats, a mother cat and three kittens, which I have designated by the letters M, X, Y and Z.

NAME	COLOR	SEX	DATE OF BIRTH
M.....	gray	female	unknown
X.....	gray	female	August, 1906
Y.....	gray	male	August, 1906
Z.....	gray	female	August, 1906

My experiments were begun in October, 1906, and concluded in March, 1907. During this time I fed the cats bread and milk

¹ This investigation was carried on under the direction of Doctor ROBERT M. YERKES, to whom I am greatly indebted for the suggestion of the problem and general method.

² The Imitative Tendency of White Rats. *Journal of Comparative Neurology and Psychology*, vol. 16, pp. 333-361. 1906.

and raw meat, with the occasional addition of some vegetables. They were fed only once a day, and the feeding time was immediately after the experiment. Enough bread and milk were given to keep the animals in good condition, and the raw beef was used principally as a reward for the performance of the required act. In all the experiments the trained cat was fed each time it performed the act which the situation required. All of the cats were perfectly tame and very active.

The general method of testing the imitative tendency of cats was as follows: Either separately or together the cats were given opportunity to learn to perform a certain act or series of acts. In case all learned it of their own initiative no tests of imitation could be made, but if one, or more, of the individuals failed, after abundant opportunity, to discover the appropriate mode of reaction, it was given a chance to learn by watching another cat perform the act.

II. EXPERIMENTS.

Experiment 1. Jumping from Box to Table.

Method.—A box, open on one side, was placed upon a table 81 cm. high. A second table 10 cm. lower was placed 56 cm. from the first. The act to be performed was to jump from the box to the meat, which was placed in plain sight on the lower table.

Results.—X, who was put into the box alone, was afraid to jump. M was put in with her, and she saw M jump from the box to the table five times, but still she was afraid to follow. Y and Z were tested in like manner with the same result. I now drew the lower table 8 cm. nearer the first, and put the three kittens into the box together, but still they were afraid to jump. M was now put in with them. The second time she jumped to the meat, X followed her. When X was put back with Y and Z she jumped down at once, and in less than a minute was followed by Z. After Y saw Z jump to the meat five times he jumped to the floor. No further trials were made.

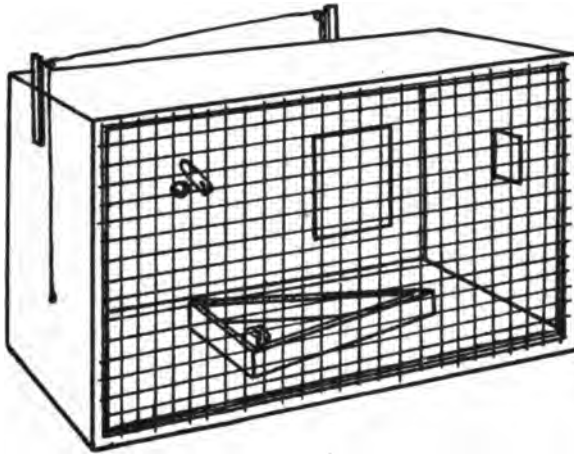
Experiment 2. Opening Door by Pulling Knot.

Method.—A wooden box (Box I) 73 cm. long, 50 cm. wide, and 56 cm. deep was closed on one side by a door of wire netting of half inch mesh. Near one end of the opposite side was a door (20 x 15 cm.) which was held shut by a wooden crossbar. From the end of

this bar a string passed up over the box and entered it at the middle of the end farthest from the door. To open the door it was necessary for the cat to pull a knot at the end of the string. The knot was close against the inside of the box (see Fig. 1).

Results.—By fastening a piece of meat to the knot I taught M to open the door. At the end of the fourth day, the association between the pulling of the knot and the opening of the door seemed to be well formed.

X, Y and Z were put into the box together. In less than five minutes X was pulling the knot. With Z watching, X went to the



BOX I.

FIG. 1.

knot, seized it and pulled hard enough to open the door. After they had been fed and put into the box again, Z pulled the knot first. X then tried it, and finally Y seized it and succeeded in opening the door. When they were put back Z at once opened the door by pulling the knot. Left in the box alone for ten minutes, Z did not get out again.

The following is Z's record for the next two days when in the box alone. Z learned to get out in less time than it required to teach M.

Oct. 27 she got out,
1st time in 3'
2d time in 1'

Oct. 28,
1st time in 2'
2d time in 30"

X and Y were now tested separately. The following table gives the time each was in the box alone.

DATE	X	Y	DATE.	X	Y
Oct. 26.....	20'	20'	Oct. 31.....	30'	30'
Oct. 27.....	20'	20'	Nov. 1.....	25'	25'
Oct. 29.....	30'	30'	Nov. 3.....	30'	30'
Oct. 30.....	30'	30'			

Neither succeeded in getting out. On Nov. 2 I put them into the box together. Y found the knot and opened the door. As soon as X saw Y pulling the knot she took hold of it and pulled. After having been put back they pulled at the knot turn about for a few minutes, and then they gave up.

Tables 1, 2 and 3 show how quickly the cats learned to open the door when they were given an opportunity to imitate.

In the tables I have given the number of times that a certain act was performed or witnessed by the subjects of the experiment, and the time which the imitator consumed in performing the act. In Table I (Y imitating Z), for example, the second column gives the number of times that Z got out of the box; the third column, the number of times that Y saw Z escape; the fourth column, the number of times that Y got out when given an opportunity to imitate by being left in the box alone, and the fifth column, the time required by Y (the imitator) in escaping.

TABLE I.
Y imitating Z.

DATE	Z GETS OUT	Y SEES	Y GETS OUT ALONE	TIME
Nov. 7.....	1	1		
Nov. 7.....			1	5'
Nov. 7.....			1	5'
Nov. 7.....			1	5'
Nov. 8.....	1	1		
Nov. 8.....			1	1'
Nov. 8.....			1	18'
Nov. 8.....			1	4'
Nov. 8.....			1	1'
Nov. 8.....			1	1'
Nov. 8.....			1	1'30"
Nov. 8.....			1	2'
Nov. 8.....			1	45"
Totals.....	2	2	11	

TABLE II.
X imitating Z.

DATE	Z GETS OUT	X SEES	X FOLLOWS Z OUT	X GETS OUT FIRST	X GETS OUT ALONE	TIME
Nov. 5.....	1	1	1		1	7'
Nov. 5.....					1	3'
Nov. 5.....	2	2	1	1	1	5'
Nov. 6.....	5	5	1	4		
Nov. 7.....	5	5	1	4		
Nov. 8.....	2	2		2		
Nov. 9.....					1	2'
Nov. 9.....	2	1		2	1	1'
Nov. 9.....	2	2	1	1		
Totals.....	19	18	5	14	5	

TABLE III.
X imitating Y.

DATE	Y GETS OUT	X SEES	X FOLLOWS Y OUT	X GETS OUT FIRST	X GETS OUT ALONE	TIME
Nov. 10.....	2	2	1	1		
Nov. 10.....					1	1'
Nov. 10.....					1	1'
Nov. 12.....	5	5		5		
Nov. 12.....					1	1'
Nov. 12.....	1	1		1		
Nov. 12.....	2	2		2		
Nov. 13.....	6	6	3	3		
Nov. 14.....	3	3	1	2		
Nov. 15.....	5	5	4	1		
Nov. 19.....	2	2	2			
Nov. 19.....					1	5'
Nov. 19.....					1	1'
Nov. 19.....	4	4	4			
Nov. 20.....	1	1	1			
Nov. 20.....					1	3'
Nov. 20.....					1	1'
Nov. 20.....					1	1'
Nov. 20.....					1	1'
Nov. 21.....					1	15'
Nov. 21.....					1	2'
Nov. 21.....	2	2	2			
Nov. 22.....					1	6'
Nov. 22.....	1	1		1		
Totals.....	34	34	18	16	12	

Z was used a few times instead of Y. The conduct of X was just the same whichever cat was used. During the trials of the first two or three days X imitated Z very closely. Sometimes,

even after Z had opened the door, she stayed behind long enough to pull the knot before following her out. Frequently X started for the door when Z or Y began to pull the knot. She looked back and forth from the knot to the door until the door opened then she dashed out ahead of the other cat. She seemed to understand that pulling the knot opened the door. At other times she quietly looked on while Y opened the door, and then followed him out. As she made but little effort to get out when in the box alone I tried to arouse her to greater activity by spreading a wet towel over the bottom of the box, but this expedient failed to produce the desired result.

Experiment 3. Opening Door by Turning Button and Pulling Loop.

Method.—A door of wire netting extended the full length of one side of a wooden box (Box II) 72 cm. long, 47 cm. wide, and 48 cm. deep. In one end of this box, 5 cm. above the floor, a small door (15 x 17 cm.) was made. This door was constructed of wire netting so that food placed on the outside of the box could easily be seen. The door was opened from the inside by turning a wooden button and pulling a loop which was concealed by the button. The button was 8 cm. to the right and a little above the door.

Results.—Z was in the box alone:

Nov. 1.....	30'	Nov. 5.....	30'
Nov. 2.....	30'	Nov. 6.....	30'
Nov. 3.....	30'	Nov. 7.....	30'

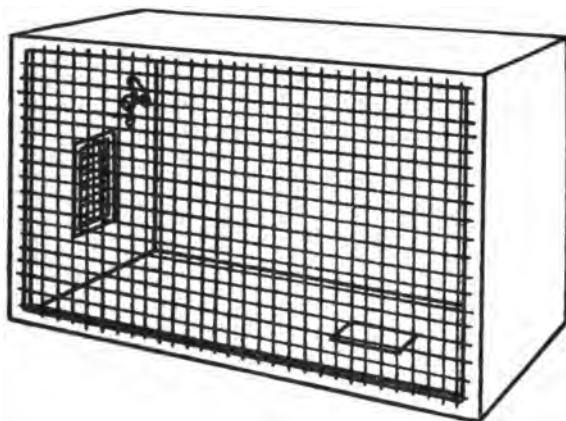
She turned the button several times during the first two days, but she did not pull the loop. During the last four days she did not touch the button. Nov. 7, after Z had been in the box alone for thirty minutes without touching the button, X was put in with her. They got out four times in less than fifteen minutes. The first two times X turned the button and Z pulled the loop, but the last two times Z both turned the button and pulled the loop. Nov. 8, Z, while alone in the box, did not even touch the button, but on Nov. 9 she succeeded in getting out in fifteen minutes. After being put back she did not get out again in thirty minutes. However, after X was put in with her they succeeded in getting out in twenty-five minutes. X turned the button and Z pulled the loop. Nov. 10, Y was in the box alone for thirty minutes and in

with Z for fifteen minutes. Neither got out although X did turn the button. Nov. 12, Y got out in less than five minutes, but when put back he did not get out again in forty-five minutes. Although X was now put in with him they did not succeed in getting out. Nov. 13, Y was in the box alone for thirty minutes and in with Z for ten minutes, but neither got out. On Nov. 14, Y, although left in the box alone for thirty minutes, did not even touch the button. After X and Z were put in with him they got out:

1st time in 5'
2d time in 10'
3d time in 3'

4th time in 1'
5th time in 1'
6th time in 1'

The first time Z turned and closed the button; then X turned the button and Z pulled the loop. The second time Z turned the



BOX II.

FIG. 2.

button and both X and Z pulled the loop. The third time Z turned the button and X pulled the loop. The last three times Z both turned the button and pulled the loop. In all these trials Y merely looked on. Z was taken out and X and Y were left in the box together for fifteen minutes, but they made no efforts to get out. Nov. 15, Y saw Z open the door four times. Each time Z opened the door both were fed, then Y was put into the box alone for five minutes. During these four trials Y touched the button but once, but after Z had turned the button the fifth time Y jumped up and pulled the loop, thus opening the door.

After being put back, he went directly to the button, turned it and pulled the loop. He now opened the door five times in less than five minutes. The association seemed to be perfectly formed.

TABLE IV.
X imitating Y.

DATE	Y GETS OUT	X SEES	X FOLLOWS Y OUT	X GETS OUT FIRST	X OPENS DOOR	TIME
Nov. 16.....	2	2	2			
Nov. 16.....					1	7'
Nov. 16.....					1	7'
Nov. 16.....	2	2	2			
Nov. 17.....	2	2		2		
Nov. 17.....					1	2'
Nov. 17.....	3	3	3			
Nov. 22.....					1	10'
Nov. 22.....					1	1'
Nov. 22.....					1	1'
Nov. 22.....					1	1'30"
Nov. 22.....					1	15"
Totals.....	9	9	7	2	8	

Each time X followed Y out she was fed and then put back alone for five minutes. If she did not get out during that time Y was put in with her again. However, the first two times X opened the door Y was in the box with her. Y first turned the button then X pulled the loop.

TABLE V.
M imitating Y.

DATE	Y GETS OUT	M SEES	M FOLLOWS Y OUT	M GETS OUT ALONE	TIME
Nov. 16.....	6	3	6		
Nov. 19.....	7	7	7		
Nov. 20.....	7	7	7		
Nov. 25.....	6	6	6		
Nov. 22.....	7	7	7		
Totals.....	33	30	33		

M did not watch Y very closely until he had opened the door several times, then she began to pay close attention, especially when he went to the button. In all the tests she had with Y she did not once attempt to turn the button. Generally she was inactive when in the box alone. During the first trial on Nov. 28 she scratched at the loop after X had turned the button. The

TABLE VI.
M imitating X.

DATE	X GETS OUT	M SEES	M FOLLOWS X OUT	M GETS OUT ALONE	TIME
Nov. 22.....	5	5	5		
Nov. 28.....	4	4	4		
Nov. 28.....				1	1'
Nov. 28.....				1	1'
Nov. 28.....				1	45"
Nov. 28.....				1	30"
Nov. 28.....				1	1'
Nov. 28.....				1	15"
Totals.....	9	9	9	6	

second time she was put back after following X out, she turned the button and scratched at the loop; but it was not until X had opened the door four times that she pulled the loop hard enough to open the door. She always pulled the loop with her claws, whereas X generally used her teeth.

Experiment 4. Getting Food by Turning Button.

Method.—A hole three-fourths of an inch in diameter was bored in the middle of Box I. This hole was covered both on the inside and outside of the box by wooden buttons. Meat was placed in the hole from the outside. To get the meat the cat had to turn the inside button (see Fig 1).

Results.—X when put into the box turned the button in less than five minutes.

TABLE VII.
M imitating X.

DATE	X GETS MEAT	M SEES	M GETS MEAT	TIME
Nov. 23.....	7	7		
Nov. 26.....	7	7		
Nov. 27.....	1	1		
Nov. 27.....			1	1'
Nov. 27.....			1	1'
Nov. 27.....			1	2'
Nov. 27.....			1	1'
Nov. 27.....			1	30"
Nov. 28.....			1	2'
Totals.....	15	15	6	

Each day M was put into the box alone for ten minutes before X was put in with her. After X had turned the button and eaten the meat she was taken out and M was left alone in the box for five minutes. She got no meat unless she turned the button. Occasionally she smelled of the button but she made no effort to turn it until the end of the fifteenth trial.

Experiment 5. Raising Small Trap-door.

Method.—A door (7 x 9 cm.) was made in the bottom of Box II. A narrow opening was left in the front end of the door. By inserting the claws in this opening the cat could easily raise the door and get the meat placed under it. The doorway was closed on the under side so that the cat could not get out of the box.

Results.—X learned unaided to open the door in less than twenty minutes and Z learned almost as soon. Y was left in the box alone:

Nov. 26.....	20'	Nov. 30.....	90'
Nov. 27.....	25'	Dec. 1.....	30'
Nov. 28.....	20'		

Although he worked at the door more or less, he did not once succeed in getting it open, as he almost invariably scratched in the wrong place.

TABLE VIII.
Y imitating X and Z.

DATE	X OPENS THE DOOR	Y SEES	Y OPENS THE DOOR	TIME
Dec. 3.....	5	5		
Dec. 5.....	2	2		
Dec. 5.....			1	4'
Dec. 5.....	2	1		
Dec. 7.....	5	5		
Dec. 8.....	7	6		
Dec. 10.....	7	7		
Dec. 11.....	5	5		
Dec. 12.....	2	2		
Dec. 13.....	3	3		
Dec. 14.....	18	18		
Dec. 14.....			1	1'
Dec. 14.....			1	1'
Dec. 14.....			1	10"
Dec. 14.....			1	5"
Dec. 14.....			1	5"
Dec. 14.....			1	5"
Dec. 14.....			1	5"
Totals.....	56	54	8	

In the tests of imitation which were now made Z instead of X was used part of the time to open the door. The behavior of Y was just the same whichever cat was used. The general method was to take X out after she had opened the door once, and let Y try the door alone for five minutes. If he did not get it open X was then put in with him again. However, on the last day of the experiment X was allowed to open the door six times in succession before she was taken out of the box.

During the first part of the experiment Y imitated X very closely. When X was taken out he frequently tried the trap-door; but during the latter part of the experiment he only looked on while X opened the door and ate the meat. *During the first series of six trials on the last day Y merely looked on, during the second series he smelled of the door each time X opened it, and during the third series he reached through the door after X had taken out the meat. After X had been taken out of the box upon the conclusion of the third series of trials Y went to the door and opened it at once. After that he opened the door as fast as I could put in the meat and close it.*

Experiment 6. Rolling Ball into Hole.

Method.—In Box I a hole large enough to admit a tennis ball was made in the middle of the bottom of the box, 12 cm. from one end. In the middle of the end of the box next to the hole and 25 cm. above the floor a small door (6 x 6 cm.) was placed. This door, which opened inward, was held shut by a wooden crossbar. The mechanical device was of such a nature that when the ball rolled through the hole and fell into a box below, the pressure on the box raised the crossbar and permitted the door to fly open. The opening of the door exposed to view a small piece of meat which the cat easily could reach. In order to make it easier for the cat to roll the ball into the hole a wooden triangle (44 x 44 x 29 cm.) was fastened to the bottom of the box with the hole at its apex (see Fig. 1).

Results.—Below are given the periods during which the cats were given an opportunity to discover that meat could be obtained by rolling the ball into the hole.

Two or three times the ball was knocked into the hole accidentally while the kittens were playing together. Strange as it may seem, X was the only one of the kittens that showed any disposition to play with the ball. It is true that occasionally one of the

TABLE IX.

DATE	Y	Z	M, Z	M, Y, Z
Dec. 1.....		30'		
Dec. 3.....		50'		
Dec. 7.....		30'		
Dec. 8.....		30'		
Dec. 10.....			30'	
Dec. 11.....			30'	
Dec. 15.....	20'			
Dec. 17.....				30'
Dec. 22.....				45'
Jan. 1.....				60'
Jan. 2.....				60'
Jan. 3.....				60'
Jan. 4.....				50'
Jan. 5.....				60'
Total.....	$\frac{1}{2}$ hr.	$2\frac{1}{2}$ hr.	1 hr.	$6\frac{1}{2}$ hr.

kittens struck it, but never twice in succession. In one week I taught X to roll the ball into the hole from any part of the triangle.

After X had rolled the ball into the hole two or three times in succession in the presence of Y, she was taken out and Y was left in the box alone for five minutes, then X was put in with him again. This was continued until Y learned to roll the ball into the hole. Y got no meat when X rolled the ball into the hole unless he got to the door first (see Table X).

During the first few trials Y merely looked on, but gradually he reached a point where he occasionally struck at the ball when X was rolling it. The next step was to strike at it when he was in the box alone. When X got the ball almost to the hole Y gave the closest attention, and when the ball went in he dashed to the door and tried to get the meat first. Not infrequently when X got the ball almost to the hole Y knocked it in. Soon after he had reached this stage he rolled the ball into the hole when he was in the box alone.

In the case of Z the method was the same as that employed with Y, except that Z was generally fed when X rolled the ball into the hole. Only twice in the forty-one trials of Table XI did Z touch the ball. As far as I could see the only thing Z learned was to associate the opening of the door with the hole, but not with the rolling of the ball. When in the box alone she devoted most of her time to the hole. Y, on the contrary, first formed the association between the rolling of the ball and the opening of the door.

TABLE X.
Y imitating X.

DATE	X ROLLS BALL IN HOLE	Y SEES	Y ROLLS BALL IN HOLE	TIME
Jan. 10.....	6	6		
Jan. 12.....	6	5		
Jan. 14.....	10	10		
Jan. 15.....	13	13		
Jan. 16.....	12	12		
Jan. 17.....	6	6		
Jan. 17.....	2	2		
Jan. 18.....	2	2		
Jan. 19.....	9	9		
Jan. 21.....	3	3		
Jan. 21.....			1	4'
Jan. 21.....			1	1'
Jan. 21.....			1	12'
Jan. 21.....	2	2		
Jan. 22.....			1	2'
Jan. 22.....			1	1'
Jan. 22.....			1	15"
Jan. 22.....			1	15"
Jan. 22.....			1	30"
Jan. 22.....			1	45"
Jan. 22.....			1	15"
Jan. 22.....			1	60"
Jan. 22.....			1	15"
Jan. 22.....			1	10"
Totals.....	71	70	13	

TABLE XI.
Z imitating X.

DATE	X ROLLS BALL IN HOLE	Z SEES	Z ROLLS BALL IN HOLE	TIME
Dec. 12.....	2	1		
Dec. 13.....	3	3		
Dec. 14.....	4	4		
Dec. 17.....	3	2		
Jan. 7.....	1	1		
Jan. 8.....	2	2		
Jan. 9.....	6	6		
Jan. 10.....	4	4		
Jan. 22.....	4	3		
Jan. 23.....	12	7		
Totals.....	41	33		

My next method was to roll the ball into the hole four times in succession myself, and then place it in the farthest corner of the triangle, and leave Z alone with it for five minutes. Z was given a small piece of meat each time the ball went into the hole. During

the first ten or fifteen trials Z merely looked on. It was not long, however, before she began to strike the ball when it was rolling. Her interest gradually increased until finally she rolled the ball into the hole of her own accord.

TABLE XII.

Z imitating Me.

DATE	I ROLL BALL IN HOLE	Z SEES	Z ROLLS BALL IN HOLE	TIME
Jan. 24.....	25	23		
Jan. 25.....	25	24		
Jan. 28.....	20	18		
Jan. 28.....			1	1'
Jan. 28.....			1	4'
Jan. 28.....			1	30"
Jan. 28.....			1	45"
Jan. 28.....			1	15"
Jan. 28.....			1	25"
Jan. 28.....			1	31"
Jan. 28.....			1	15"
Jan. 28.....			1	15"
Totals.....	70	65	9	

For M the method was the same as that used with Z except that I rolled the ball into the hole five times in succession instead of four. During the latter part of the experiment the method was varied somewhat by giving M a chance at the ball each time after

TABLE XIII.

M imitating Me.

DATE	I ROLL BALL IN HOLE	M SEES	M ROLLS BALL IN HOLE	TIME
Jan. 25.....	15	14		
Jan. 26.....	30	26		
Jan. 28.....	25	23		
Jan. 29.....	25	23		
Jan. 30.....	25	25		
Jan. 31.....	25	23		
Feb. 1.....	25	21		
Feb. 4.....	25	24		
Feb. 5.....	26	24		
Feb. 6.....			1	1'
Feb. 6.....	22	22		
Feb. 7.....	9	9		
Feb. 7.....			1	3'
Feb. 7.....	6	6		
Feb. 7.....			6	
Feb. 8.....			20	8'30"
Totals.....	258	240	28	

I had rolled it into the hole. The second day she struck at it several times as it was rolling toward the hole. There seemed to be no method in her attempts, for several times she knocked the ball away from the hole when otherwise it would have gone in. On January 31 for the first time she struck the ball when it was not in motion. From this time on it was an easy matter to get her to strike it by tapping on the floor beside it. When she was left alone occasionally she smelled of the ball, but she spent most of her time watching me and washing herself. It was not until the last two days of the experiment that she deliberately rolled the ball into the hole.

Experiment 7. Learning to Catch Mice.

Method.—A cage 112 cm. long, 83 cm. wide, and 190 cm. high was inclosed on three sides with wire netting. A mouse put into this cage could neither escape nor conceal itself.

Results.—January 2. A large black mouse was placed in the cage with Z. At first Z very cautiously smelled of it. Then when the mouse ran she ran after it, striking it with her paw. Although she became rougher in her play during the last half hour, she did not once growl or strike the mouse with her claws. At the end of one hour the mouse was taken out of the cage uninjured.

January 3. Y was put into the cage with the same mouse for one hour. When the mouse ran he ran after it, but at first he did not touch it. After a few minutes, however, he began to strike it. When it climbed up the side of the cage he sat and watched it until it came down again. Unlike Z, he used his claws and switched his tail. During the last few minutes of the hour he did not seem to be much interested in his companion.

January 4. X was put into the cage with the same mouse for one hour. At first, like the other cats, she merely smelled of the mouse and followed it about the cage, but soon she began to strike it with her paws. A few times she seized it in her mouth. As far as I could see she never used her claws. She played with it much as she played with the tennis ball in Experiment 6. Her interest abated somewhat during the latter part of the hour. The mouse when taken out of the cage apparently was uninjured, and began to wash itself. However, two days later it was found dead in its cage, possibly from injuries received in the experiment.

February 14. Y was in the cage with a gray mouse for fifteen minutes. She followed it about striking it gently with her paws. When it ran up the side of the cage she ran up after it and brought it down in her mouth, but she did not injure it.

February 15. The same gray mouse was put into the cage with Z for twenty minutes. The mouse climbed up to the top of the cage. Z went up and smelled of it four times before she knocked it down with her paw. She did not pay very much attention to it during the last five minutes.

February 15. Y was put in with the mouse for twenty minutes. He soon discovered it up at the top of the cage. After he had gone up and smelled of it three times he seized it with his teeth and threw it down. He switched his tail and his claws rattled on the floor as he ran after it, but he never growled. In all of these trials the cats had not been fed meat for at least twenty-four hours.

February 16. A white mouse was put in with X. The cat played with it as usual. After a few minutes M (the mother cat) was put into the cage with X. She killed and ate the mouse while X looked on. X did not dare to approach as M growled very ominously whenever X moved. After M had finished eating the mouse I took her out and put another mouse in with X. She played with it just as she had played with the other one. I could not see that her behavior was influenced in the least by the tragedy she had just witnessed. When Z was put into the cage with her X seized the mouse in her mouth whenever Z approached, but as long as Z did not move she played with it as usual. When the mouse was given to Z she would not let X have it. After a few minutes Z was taken out and M was put in with X. M killed the mouse at once and began to play with it. She let X have it, but the latter would not eat it, until M had exposed the raw flesh; then she ate it at once. M was now removed and another mouse put in with X. She played with it as usual, but made no attempt to kill it.

February 19. A white mouse was put into the cage with X for ten minutes. She was no rougher with it than usual. But when Y was put in with her she seized the mouse and began to growl. When the mouse ran toward Y he did not attempt to seize it even when it was nearer to him than it was to X. After removing Y, I fed M a little meat in sight of X. She at once left the mouse,

went to the side of the cage next to M and began to mew. Apparently she did not realize that she had fresh meat at her disposal. A mouse was now given to M, who killed and ate it while X looked on. X was allowed to smell of the blood on the floor; then another mouse was given to her. She played with it as usual. Apparently she had not profited in the least by M's experience.

Next Y was tested with the same mouse. He was not as rough as usual in his play. I now put M in with him. She killed the mouse and began to eat it. After she exposed the raw flesh I gave it to Y who ate it at once. After he had finished eating it I gave him another mouse, but he did not attempt to injure it. Five minutes later Z and X were put in with Y. Growling fiercely, he seized the mouse. In fifteen minutes he had killed and eaten it.

February 20. A white mouse was put into the cage with Z. As the mouse tried to bite her she picked it up and tossed it about as if it were a rag ball. She did not seem to be angry in the least. When X was put in with her she growled and seized the mouse, but after a few minutes she let X have it. After they had played with it turn about for a few minutes, Y was put in with them. He killed and ate the mouse while they looked on. He was now taken out and a brown mouse was put in with X and Z. X seized it and killed it almost instantly. In less than five minutes she had eaten it. X was now removed and a brown mouse was put in with Z. She played with it but did not attempt to kill it.

February 21. Z played more gently with the mouse than usual. X was now allowed to kill and eat the mouse while Z looked on; then Z was given another mouse. She played with it a little while, then refused to take further notice of it. I put M, X and Y on the outside of the cage but they did not arouse Z in the least. She simply ignored the mouse.

March 6. Z played very gently with a mouse, until I put X in with her, then she seized it; but X soon succeeded in getting it away from her. After X had almost killed it, I gave it to Z again. She seized it savagely and held on to it, growling almost continuously. In less than a minute the mouse was dead and Z had begun to eat it.

March 7. A big brown mouse was given to Z. She played with it but did not attempt to injure it. Fifteen minutes later X was allowed to kill the mouse while Z looked on. After she had half eaten it I gave it to Z who soon finished it.

March 8. Z played with a mouse but made no attempt to kill it. But as soon as she saw X and M, who were now placed on the outside of the cage, she seized the mouse and began to growl fiercely. In seven minutes she had killed and eaten it.

March 13. Z was put into the cage alone with a mouse. In fifteen minutes she had killed and eaten it.

Experiment 8. Getting Meat out of Bottle.

Method.—In the opening occupied by the small trap-door in Box II a pint milk bottle was firmly fastened. It was partly filled with cloth so that the cat could easily reach meat which was placed on top of the filling.

Results.—M got the meat in four minutes. Y was successful in ten minutes, but Z failed completely, although she worked hard for twenty minutes. Her method was to stick her nose into the bottle and then reach for the meat with her paws on the outside. She also tried to get her nose and paw into the bottle at the same time.

X tried the same tactics as Z, except that she balanced herself with her nose in the bottle, and then reached for the meat simultaneously with both paws.

The next day Z again failed to get the meat in a trial of twenty minutes. After she had ceased trying X was put in with her. Although she went to work very energetically at the bottle she did not succeed in getting the meat, but her efforts did arouse Z to renewed efforts with the result that this time she was successful. She was now removed and X was left in the box alone for thirty-five minutes. She did not get the meat. On the following three days X was tested alone for the following periods:

Jan. 21	60'
Jan. 22	20'
Jan. 25	40'

She did not once succeed in getting the meat. After X had been in the box alone for forty minutes during the trial of January 23 I put Y in with her. *She watched Y very closely as he reached into the bottle and took out the six pieces of meat. After Y was removed X went to the bottle and got the meat in less than two minutes.* At first she used her old method, but finding that did not work she went at it as Y had done. In further trials she got the meat as skillfully as did X and Y.

Experiment 9. Getting down from Top of Cage.

Method.—The kittens frequently climbed up on top of the cage which was used in Experiment 7, but they could not get down without help. I arranged a broad board (170 cm. long) in such a way that by jumping 40 cm. to this board, walking down it to the lower end, and then jumping 60 cm. they could reach the floor.

Results.—All three cats were placed on top of the cage, then meat was thrown on the floor in front of it. They were greatly excited. X got down by the way of the board in three minutes; Y doubled up to follow X, but his courage failed. Z who did not see X get down now jumped down as X did. Y looked on, and again doubled up to jump, but his courage was insufficient. After seeing X get down two more times he followed her down.

III. DISCUSSION OF RESULTS.

In the discussion of imitation it is essential that the term be defined objectively if it is to have much value for the comparative psychologist. That is, it must be so defined that the imitation is always from the standpoint of the observer. I think that MORGAN's use of the term is satisfactory in this respect, for he says, "in the case of an imitative action the stimulus is afforded by the performance by another of an action similar in character to that which constitutes the response."³ The acts of organisms are generally classified as instinctive, voluntary, and habitual. For each class there is a corresponding type of imitation.

As an illustration of instinctive imitation MORGAN cites the case of a hen pecking on the ground, and the chick imitating her action. It is the pecking of the mother hen that acts as a stimulus for the instinctive act of the chick.

Automatic or habitual imitation I use to designate those cases where the imitative act is simply an involuntary performance of an acquired, as opposed to an instinctive act. An example of this is the involuntary whistling of a tune that one hears another whistling. Here the act is involuntary, but not instinctive.

On the subjective side voluntary imitation is conscious purposive imitation. The act of another is imitated with a definite end in view. The test for this kind of imitation is refusal to imitate until

³ MORGAN, C. L. *Habit and Instinct*, p. 168. London. 1896.

the benefits that would come from imitating have been perceived or experienced. For example, suppose two cats are put into a box together. One cat opens a door by turning a button, while the other cat merely looks on. Both pass out and are fed. If now, when the second cat is put back it goes to the button and turns it, thus opening the door, this would be an instance of voluntary imitation.

In the nine experiments with cats which have been described I have found instances of imitation. So the question is not, "do cats learn by imitation?" but instead, "what is the nature and extent of their imitation?"

In the first place, what evidence is there for voluntary imitation? In Experiment 4, M refused to turn the button until she had seen X turn it several times and get meat. Her failure was not due to lack of hunger, for after she turned the button once she continued to turn it as fast as I could put the meat in and close the hole.

I consider this a fair example of voluntary imitation, for M refused to turn the button until she had seen X repeatedly get meat by turning it. If it were merely instinctive imitation we should have expected M to scratch at the button while X was turning it, but this she did not do. She merely watched X, and when X was taken out of the box she went to the button and turned it. Of course it may be said that the act was purely accidental, but her manner seemed to indicate that such was not the case.

In Experiment 6, Y refused to roll the ball into the hole until he had experienced the results that came from performing the act. It was then, and not until then, that he began to roll the ball and watch the door. In Experiment 7, it was not until X had seen several mice killed and had eaten two that she seized and killed a mouse when it was put into the cage with her.

It seems to me the fairest way of interpreting these cases is to admit that they are instances of voluntary imitation of a low order. I say of a low order, because the imitation did not occur until the required act had been performed many times by the trained animal. In many cases I think it is not so much the association of the trained-animal-performing-the-act with the-getting-of-food, as it is an association of the-act-being-performed with the-getting-of-food. For example, in Experiment 6, Y, I think, first formed the association of X-rolling-ball with the-getting-of-food, but as the act was repeated by X the ball seemed more and more to attract

the attention of Y until the association changed to rolling-of-ball with getting-of-food. The facility with which an animal imitates will depend, in large measure, upon how closely it attends to what the trained animal is doing. If it does not watch closely what is being done, the association is almost sure to be the-trained-cat with the-getting-of-food. And if this association is once stamped in, it is doubtful whether imitation can occur.

In voluntary imitation the act is performed not merely from impulse, but for the food or freedom that may result from its performance. In instinctive imitation, the performance of the act by the imitatee is sufficient stimulus to call out a similar response on the part of the imitator. In other words, the animal sees and then finds itself performing the act.

The subject of instinctive imitation has been passed over very hurriedly by most students of animal behavior. They seem to conclude that if a high type of voluntary imitation does not exist among the lower animals, imitation is of but little importance. Now I am convinced from my work with rats and cats that instinctive imitation is a factor of very great importance in the mental development of these animals. In nearly all my experiments instances of instinctive imitation were common. For example, in Experiment 2, Z seeing X pull at the knot, went to it, seized it and pulled hard enough to open the door. After they were fed and put back into the box, Z pulled the knot first, X then tried it, and after she had stopped, Y seized it and pulled hard enough to open the door. It was through instinctive imitation that the cats learned to get out of the box. X was the first cat to find the knot, yet it was Z imitating X who opened the door. The next time Y opened the door after Z had pulled the knot. When they were put back for the third time Z went directly to the knot and opened the door.

Z, being the most intelligent of the three cats, was the first to acquire the association between the pulling of the knot and the opening of the door. The other two cats subsequently learned to get out by imitating Z. I think this experiment well illustrates the importance of instinctive imitation.

Experiment 3 is also very illuminating in respect to instinctive imitation. After Z had been thoroughly tested without succeeding in getting out, X was put in with her. They got out four times in less than fifteen minutes. The first two times X turned the

button and Z pulled the loop. The last two times Z both turned the button and pulled the loop. Here Z learned to get out of the box by imitating X, the less intelligent of the two. Y learned from Z, and X learned from Y.

Let us consider the nature of the associations formed in a case of instinctive imitation. X knows how to get out of the box. Y has been tested but has not succeeded in learning to get out. Y sees X pulling at the knot and he instinctively scratches at it a little, until X succeeds in pulling it hard enough to open the door. Both pass out and are fed. A few more times X opens the door, assisted in part by Y. Now if Y is put into the box alone and he opens the door by pulling the knot what associations have been formed? The first time he imitated X in scratching at the knot, the act was an instance of instinctive imitation, for he had no knowledge of an end to be attained beyond the mere performance of the act. But when simultaneously with Y's scratching, X opens the door, and they both secure food, the condition has been provided for the formation of an association between the scratching at that spot and the opening of the door. If upon being put back Y should scratch and thus open the door, the association formed would be quite independent of X, for the first time X opened the door Y did not associate it with the pulling of the knot by X, but with his own scratching at or near the knot. The first time Y scratched at the spot the stimulus was X scratching at that spot; the second time the stimulus was food to be obtained.

Not only is instinctive imitation of great importance in itself, but it is also important in that it leads up to voluntary imitation. It seldom happens that a cat learns by going through the act with the trained cat only once; generally it must see and help the imitator perform the act many times before it is able to perform it alone.

Now in all these trials, after the first one, the imitator either looks on or participates in the act with a knowledge of the end to be attained. Here we have to some extent voluntary imitation, for the imitator is influenced not only by his own movements, but by seeing the other cat perform similar movements. The next step in the learning process is to form the association by observing the other cat perform the act and by sharing with him its benefits.

Let me point out more clearly the different steps involved in learning by imitation.

1. Through instinctive imitation the cat performs the act once. As far as performing the act the second time is concerned the cat now is on the same basis as the animal that has accidentally performed the act once. But if the trained cat continues to perform the act, then the imitator has in addition to its first experience the experience of the trained cat to help in stamping in the association. Here it is that the transition to voluntary imitation occurs.

2. Voluntary imitation, where the imitator gets food each time the imitator performs the required act (Experiment 2).

3. Voluntary imitation, where the imitator is not fed when the imitator performs the required act, but is free to imitate (Experiment 4).

4. Voluntary imitation, where the imitator observes from another compartment the imitator perform the required act. For reasons already stated⁴ I do not think that imitation of this kind is to be found in rats and cats.

In the course of these experiments there were many instances of automatic imitation. In Experiment 6, Z formed the habit of looking into the hole in the bottom of the box. If another cat looked into the hole, she would almost invariably take a look. Again, when I changed the nature of the mechanism, yet used the same box, the trained cat went to the place where the string had been and scratched there. After doing this a few times she made no further efforts, but if later another cat went to that same spot and scratched the first went and did likewise.

Evidently automatic imitation enables an animal to retain what otherwise would soon be forgotten. Unlike human beings, they are very dependent upon external stimuli to enable them to utilize their past experience. For this reason automatic imitation plays an important part in enabling them to retain and utilize their past. If four or five kittens are taught to perform an act that results in the securing of food, the chances are that such an act will be performed by the individual members of that group much longer if they are kept together than it would if they were separated. For when one performs the act, the others automatically or voluntarily imitate him. In this way acts that have once been learned may be retained and made the basis of the performance of more complex acts.

⁴ The Imitative Tendency of White Rats. *Journal of Comparative Neurology and Psychology*, vol. 16, p. 360. 1906.

It frequently happened during these experiments that the imitation was not exact. For example, in Experiment 3 M learned to pull the loop from imitating X, yet M always pulled the loop with her claws whereas X generally used her teeth. THORNDIKE would not call this a case of imitation, for in commenting on the results of his experiments with cats he says: "Good evidence that he did not imitate is the fact that, whereas 1 (whom he saw) pulled the loop with his teeth, 7 pulled it with his paw."⁵

To say that this is not a case of imitation is as absurd as to say that the small boy does not imitate his father because his father uses his right hand to drive a nail, whereas he, the small boy, being left-handed, uses his left hand. Just as the stimulus for the small boy was his "father driving a nail," not his "father driving a nail with his right hand," so in this experiment the stimulus for M was "X pulling the loop," not "X pulling the loop with her teeth."

In Experiment 6, Z and M learned to roll the ball into the hole from watching me do it. From the way they acted I have reason to think the association formed was, ball-rolling-into-hole with getting-of-meat. Here the attention was centered on the most striking element of the complex, the rolling of the ball. Their attention was focused, not so much upon what I was doing as upon what the ball was doing. As soon as the ball began to roll they lost all interest in me and watched it. This was especially noticeable after I had performed the act several times. This simply shows that certain elements of a given complex are likely to be singled out, and these enter into the association to the exclusion, in large measure, of other elements.

I am also led to believe that cats are credited with more instincts than they really possess. It is commonly reported that they have an instinctive liking for mice, and that mice have an instinctive fear of cats. It is supposed that the odor of a mouse will arouse a cat, and that the odor of a cat will frighten a mouse. My experiments tend to show that this belief is not in harmony with the facts. When cats over five months old were taken into the room where mice were kept they did not show the least sign of excitement. A cat would even allow a mouse to perch upon its back, without attempting to injure it. Nor did the mice show any fear of the cats. I have seen a mouse smell of the nose of a cat without showing any sign of fear.

⁵ THORNDIKE. Animal Intelligence. *Psychol. Review, Monograph Supp.*, vol. 2, no. 4, p. 58. 1898.

It was not until the mouse began to run that the interest of the cat was aroused. The cat then ran after it, playfully striking it with her paw, becoming rougher the longer she played with it. The instinct seems to be for the cat to run after that which runs from it. I think it is evident from Experiment 7 that it is through imitation that the average cat learns to kill and eat mice. If this is true, it shows the extreme importance of imitation in the mental development of the cat. Furthermore it indicates that much that has commonly been attributed to instinct is, in reality, due to imitation.

However, a potent factor in this learning to kill mice is the mere presence of another cat. As a rule, when one of the cats was left with a mouse it merely played with it without showing any signs of anger; but the moment another cat approached its attitude changed at once. It now seized the mouse and began to growl. In this way one kitten may happen to kill a mouse in trying to keep another kitten from getting it.

My experiments have demonstrated furthermore, the fact that important individual differences appear in cats of the same litter. One individual has more intelligence than another, and there are marked variations in the learning ability of the same individual in different experiments.

To sum up, I think my experiments have shown: (1) that voluntary imitation of a certain type exists in cats; (2) that cats, to some extent, imitate human beings; (3) that instinctive imitation in cats is more important than students of animal behavior have supposed; and (4) that cats do not instinctively kill and eat mice, but learn to do so by imitation.

ORIENTATION IN THE WHITE RAT.

BY

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WITH ONE FIGURE.

In a previous paper¹ the present writers advanced the conclusion that kinæsthetic and organic data play the fundamental rôle in the reactions of the white rat to the maze. This conclusion was reached by eliminating the other senses singly or in groups. It was not denied that the rat may occasionally use the data from these other senses or that it could use them if the occasion demanded. The present experiments attempt to supplement this conclusion. In them, conditions were imposed upon the rat which would tend to bring the kinæsthetic factor into strong relief if, as assumed, it does possess fundamental importance in the determination of conduct within the maze. Two experiments were made: (1) After learning the maze, starting always from *O*, the rats were placed in the positions² marked x_1 , x_2 , x_3 , in the true pathway headed in either the right or the wrong direction and their method of obtaining orientation under these novel conditions was observed. The conclusion mentioned above was then theoretically discussed in the light of the new facts thus obtained, to see if difficulties and contradictions appear. (2) After the reactions to the maze became automatic, certain of the runways were either shortened or lengthened. The disturbing effect of these alterations upon the rats' conduct and their methods of learning to adjust themselves to the new conditions were observed. The two experiments will be discussed in order.

EXPERIMENT I.

THE EFFECT OF STARTING THE RAT AT DIFFERENT POSITIONS.

When the trained rat is put down in the maze at unfamiliar starting points, several possibilities of conduct are open to it:

¹ WATSON, J. B., *Psychological Review*, Monograph Supplement, vol. 8, no. 2, 1907.

² See cut of maze, p. 28. A similar but unsatisfactory test was reported in the previous paper. See p. 81, *loc. cit.*

(1) the animal may not have profited in the least by its previous experience in the maze; the situation may offer a problem *de novo*; (2) the rat may orient itself immediately as does a human

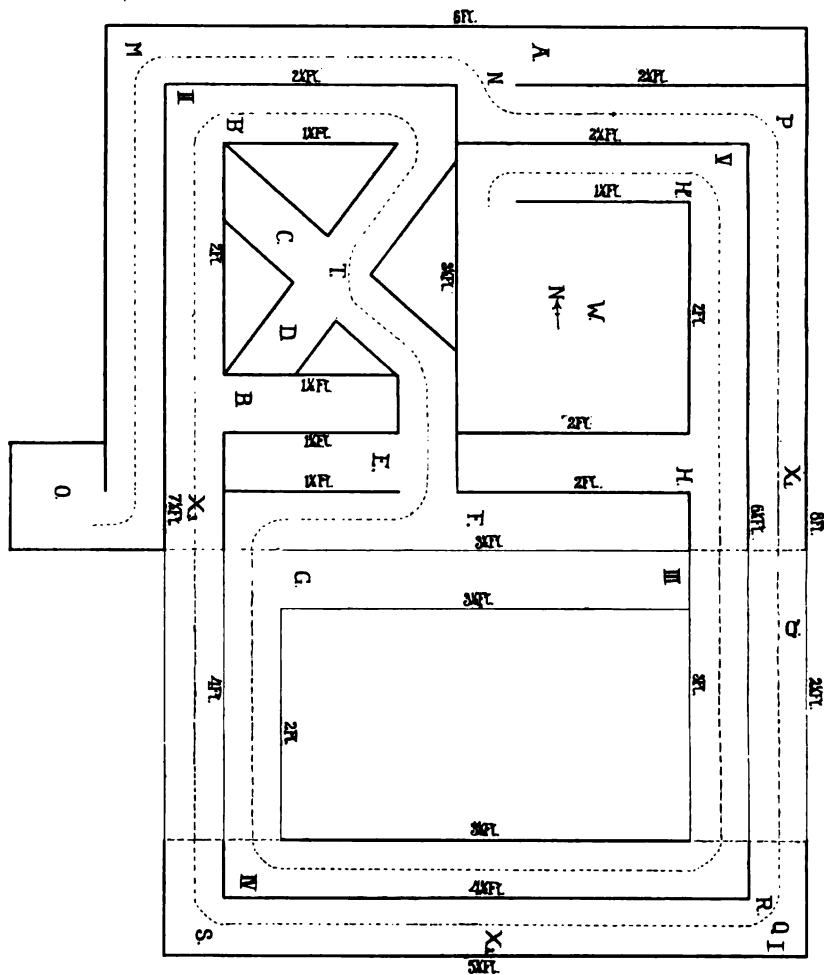


Fig. 1.

being, when, in a partially strange situation, he suddenly finds some thoroughly familiar landmark; (3) immediate orientation may not occur, and yet the situation may not be entirely new to the rat; it may exhibit some random movements before starting

properly; but its conduct might be wholly different from an animal which had not previously learned the maze; (4) if the last condition obtains, can the rat learn in time to orient itself immediately when put down at random at any one of two, three or four such starting places?

On the basis of results obtained from our work during the past summer, which is presented in detail on page 33, combined with the previous work of WATSON³ and of CARR,⁴ we are ready to give more or less satisfactory data bearing upon the above questions. (1) The situation does not present a problem *de novo*. (2) Nor does immediate orientation occur. (3) There is a period of random effort; the rat may wander about, turn around in the alleys several times or run up and down the pathway for a variable distance, acting as though lost or in a new situation. In conscious terms, its behavior suggests uncertainty, perplexity, and lack of confidence. Finally, a change of behavior is observable. The suggestion of perplexity and uncertainty is gone, the rat starts off with a sudden burst of increased speed and every movement thereafter is characterized by the precision and regularity which mark the functioning of an automatic habit. The remaining part of the maze is run in the normal and habitual manner. This change of conduct has been termed "getting the cue." The "cue" may come suddenly while the animal is running backward in the maze with irregular speed; the rat may suddenly stop, turn quickly and start off at full speed toward the food-box. The change often comes gradually, especially when the animal starts off running in the right direction. After the cue has apparently been obtained, it may be lost for a time and again found after a short interval; however the cue once obtained is rarely lost. Furthermore, once the animal attains orientation, it traverses the rest of the maze without error. This change from random to controlled activity is striking and characteristic, but extremely difficult of description except in anthropomorphic terms. (4) The rat can learn with a sufficient number of trials to orient itself immediately, starting at random from any one, two, or three definite positions in the maze. The number of trials necessary to accomplish this feat has not been determined accurately. One set of rats learned to start from any one of six cul-de-sacs on the

³ *Ibid.*, pp. 82 and 83.

⁴ Heretofore unpublished.

basis of an average of eighteen trials for each animal. This would imply that under these conditions, three trials per rat were required by it in order to learn to start at random from any one of six cul-de-sacs. A greater number of trials, however, is necessary when the animal is forced to start at random from six such positions in the true pathway. In the latter case, orientation at these positions does not become immediate in less than five or six trials.⁶

With these facts bearing upon the behavior during the establishment of orientation before us, we may now well ask the question: how does the rat attain orientation? Can he do it in terms of kinæsthetic data alone? From our previous work upon the behavior of normal, blind, and anosmic rats in tests of this kind in the Hampton Court maze, it appeared, since no difference in conduct between the normal and defective animals could be found with respect to their ability to attain orientation when put down in the maze at unfamiliar starting points, that visual and olfactory data are at least not largely employed by them as a means of controlling their movements. This conclusion is based upon the assumption that the processes employed as control by the defective rats are the same as those which would have been employed by them had they been normal. Let us suppose, for example, that a normal rat does use visual data, or the data from some other "distance" sense, for controlling his movements when the automatic (kinæsthetic-motor) character of the act is interfered with, as is the case at first when the animal is started in the maze at some point other than the customary one. What would be the nature of the orienting process? Evidently the animal would have to move at random until distinctive familiar visual or other extraorganic stimulation appeared, at which time the automatic series would be restored and the animal might thereafter have no further need for distance sense data during the remainder of the trip around the maze.

If, however, we deny to the rat the possibility (or better, the probability) of its using distance sense data in the way described above, it becomes necessary for us to answer the question: how can a kinæsthetic-motor series, which has been thrown out of gear become readjusted without control data from some other sense avenue?

If we assume that each separate "unit" (possibly a runway) of the maze affords some characteristic set of kinæsthetic impulses which can be utilized as a stimulus to secure the proper adjustment to the succeeding unit, we might have a situation where a distinctive set of kinæsthetic impulses would serve the animal for control exactly like a set of distinctive visual cues, for example. There are four ways in which distinctive kinæsthetic groups of impulses might arise. (a) Two runways may be of unequal length. (b) They may be of equal length, but occur in different positions in the total series, *i. e.*, they are preceded by different conditions. (c) They may be alike in every respect with the exception that the one is entered by a turn to the right, while the other is entered by a turn to the left. In rounding a corner at a high rate of speed, the body sways over to the inside, the weight is thrown on one side, while the feet on the outer side are braced in order to maintain equilibrium. Such differences are so gross and fundamental that it is idle to deny that they possess functional influence upon subsequent behavior. (d) The alleys may be of the same length and be entered by the same direction of turn, but present possible differences in their stimulating effect because they extend in different directions. It is difficult to conceive why and how this can be so, and the possibility is suggested only because of certain observed facts. The successful functioning of an automatic habit depends upon the rat's orientation in relation to cardinal positions. Change the direction of the path and the automatic act is disturbed to some extent. The same act accomplished in two different directions is thus *different in some way to the animal*. Thus, it is theoretically possible for the rat to adapt its behavior successfully to a series of objective conditions wholly in terms of the differences in kinæsthetic stimulation, which it offers, without relying to any extent upon data contributed through any of the distance senses. We have no intention of maintaining that the rat discriminates these possible differences in kinæsthetic values in any overtly conscious or intellectual manner, *viz.*, that they know "right" and "left" or cardinal directions, or that they consciously evaluate in any kind of terms the length of the alleys.

If, as we have assumed, the automatic behavior of the rat in the maze is governed by distinctions lying within the kinæsthetic impulses themselves, we are in a position to understand the situa-

tion presented to the rat when it is introduced into the maze at some one of these positions. The animal must perforce run up and down the alleys until it experiences some one or several of these characteristic motor situations which would give rise to the necessary stimulations to release the old automatic movement. The rat may run the length of the alleys, around corners, or traverse several alleys before getting the cue. Moreover, on this basis, one can conceive why at times the cue should be gradually attained. At such times, a summation of stimuli would be required.

On the other hand, it may with justice be argued, as we ourselves above suggested, that if the cue is received through data from some distance sense, the animal must still run about at random until it receives some one or several such characteristic stimuli. This argument cannot be met wholly, but if our own behavior under similar circumstances can by analogy be made to apply to the case of the rat, we should be allowed to assume, when our elimination experiments are considered, that this period of random activity would be much shorter when distance sense data are employed than when kinæsthetic are used. It must be frankly admitted that the purpose of our work was to see whether the facts of orientation offered insuperable difficulties to our theory rather than to attempt to rule out all possibility of the rats' receiving aid from extraorganic sense data.

This assumption granted us, our argument may now be stated as follows. If the animals orient themselves in the maze in the majority of cases by running at least the full length of one alley, by rounding corners into a second alley, or by running through several alleys before picking up the cue, the facts will be explicable in terms of the kinæsthetic hypothesis, and consequently there will be no theoretical difficulty in supposing that the rat's automatic movements in the maze as a whole are controlled by kinæsthetic impulses alone. If, on the other hand, the rats orient themselves in the majority of cases with a minimum of random movement, the facts will not be so easily explicable in terms of our hypothesis, as in terms of some other which would admit that control is inaugurated by data from some distance sense and consequently, that automatic behavior in the maze may be guided and controlled effectually as occasion demands by such means.

In order to make a careful test of the facts of orientation, sev-

eral conditions must be observed in the experiment: (1) The alleys of the maze into which the rats are introduced should be relatively long and should differ markedly in their length. (2) When placed in the maze, the animals naturally tend to spring from the hand on the run, and go for a short distance before attempting to adjust themselves to the situation. This tendency should be minimized as much as possible by holding them in position for a short time, or by allowing them to nibble a crumb of bread when released. (3) Since, with successive attempts, the rats will gradually learn to make immediate orientation, only a few trials for each position should be given. The series of tests, the results of which are given in the paper previously referred to, are faulty in the first and third respects. We have repeated the experiment in order to eliminate these possible sources of error.

In order to meet the conditions required under (1), a new maze was constructed the plan and dimensions of which are represented in the cut. The alleys are six inches wide and six inches deep. Finished lumber was used, the cracks in the floor were filled with putty, and the whole maze was given three coats of white paint. The maze was constructed so that it could be sawed across at the dotted lines and divided into three sections for the purpose of the second experiment. The maze was not so divided until the first experiment was completed. The cut represents the maze as used, with the exception that the opening into the cul-de-sac *B* was closed. The experiment was conducted out of doors in an enclosed yard. The rats were introduced into the maze at the positions x_1 , x_2 , and x_3 . Two of these alleys are seven and one-half feet long, while the third is two feet shorter. This allows the animals to run a distance of two and one-half to three and one-half feet in either direction from the starting place before a turn is possible or necessary. The experiment was started with twelve rats, but four became sickly and unreliable in conduct and were discarded. The group consisted of three normal males, two blind males and three normal females. After the rats had been thoroughly trained, the experiment was started each day by giving them a preliminary run through the maze and then introducing each rat separately at x_1 with wrong orientation, at x_2 with correct orientation, and at x_3 with wrong orientation. By "wrong" orientation, we mean that the rats were headed back towards the starting box, *O*. This procedure was followed the second day

with the exception that the orientation for each position was reversed. Thus three trials were given each rat per day, and the same orientation for any one position was repeated every other day. Not more than a total of twelve trials was given to any one rat. These varied conditions were designed to eliminate the possibility of *learning* to react immediately to a given position. An accurate account of the behavior of each rat was taken, including the changes in direction of movement, the distance traversed, the turnings inside the alleys, partial returns and the position where the rat seemed to pick up its cue. The conduct was noted by two, and sometimes by three observers. In all, 84 tests were made and the results were tabulated in statistical form.

No noticeable tendency for the rats to start in the direction in which they have been oriented was observed. They are just as likely to turn around immediately and start off in the opposite direction. Neither do they tend to start either toward the food-box, *W*, or back toward the original entrance, *O*. In other words, the direction of starting is apparently a matter of chance entirely. This fact of itself argues the lack of any immediate orientation. The situation in which they have been placed thus does not influence nor determine their conduct at the beginning of the test.

The movements in the latter part of the period of exploration are determined to some extent: The rats tend to migrate back toward the starting box, *O*. In 75 per cent of the trials, the cue was picked up somewhere between the position where they were released and the box *O*. The rats often explore on both sides of the position at which they are released, but 85 per cent of the distance traversed in the period of exploration is on the side toward *O*. This general fact may be difficult of explanation, but that some determining influence is at work is too evident to admit of doubt. The following explanation may be suggested as a possibility. In learning the maze originally, the rats explore for a distance from *O* and retrace their steps. This performance is repeated on successive trials with more extensive excursions. When the rats become lost or confused during any trial, although the maze is partially learned, they always run back toward *O*. It seems that the maze is learned in sections, as it were, and in case the rats become lost at any time, they are able to retrace their steps to more familiar surroundings. When the rat is now introduced at the position *x*, and begins to explore, the situation becomes

familiar to some extent, and the rat acts as it has been accustomed to in order to get started correctly, *i. e.*, drifts back toward *O*. Such a conception, however, leaves much to be explained.

The general statement that the situation is not entirely novel during the period of exploration and that the behavior of the rats is influenced as a result, is also supported by the fact that few errors are made, *i. e.*, errors in the sense of running into cul-de-sacs during the period of exploration. Of the 84 trials, errors occurred in but eight. Four of these errors were made by one rat. Such a percentage of errors is possible in running the maze normally. In four cases, the error occurred after the orientation had apparently been secured. But two chances for error were offered in those parts of the maze traversed during the period of exploration. In 55 of the trials, the rats passed by one of these openings leading into a cul-de-sac before securing orientation; and they often passed by the same opening several times in the same trial. Yet out of these numerous possibilities, only four cases of error of this kind occurred. The exploring movements are thus confined almost exclusively to the true pathway.

On the average, the rats turned around 2.5 corners in each trial before being able to pick up the cue; in other words, they explored fully or in part three alleys per trial before becoming oriented. Their explorations averaged a distance of 12.6 feet per trial. Inside the alleys, they changed the direction of exploration 1.3 times per trial. In only ten trials out of the 84 was the exploration confined to the alley in which they were placed and in these cases the distance traversed averaged 2.8 feet per trial, while the direction of movement was changed at least once. In 57 cases out of the 84, they went outside of the alley into which they were introduced before becoming oriented. Immediate orientation apparently occurred in seventeen trials. It is extremely doubtful whether several of these are legitimate cases of immediate orientation. A rat may by chance run forward toward the food-box, *W*, and become oriented gradually. In four of these cases, the rat went forward to the food-box, but ran hesitantly, made stops, or entered some of the cul-de-sacs. It was our policy to record under the heading of immediate orientation every case that could possibly be interpreted in that manner. As may be seen, these four trials are exceedingly questionable. In four other cases the rats turned around several times in the alley before

starting off. Nine trials were clear-cut, legitimate cases of immediate orientation. However, eight of the total number of immediate orientations were made by two rats, and the influence of the learning factor is evident in spite of the small number of trials allowed to each animal. *No immediate orientations were made during the first day. Only three cases occurred during the first half of the trials, while the remaining fourteen cases were made during the last half of the tests.*

There was a tendency for the rats to pick up the cue at distinctive points in the maze. In the 67 trials in which there was a period of exploration, the cue was picked up 13 times at *O*, 11 times at or near the corner *M*, 15 times at the turn *N*, 11 times at the corner *P*, 7 times at the corner *R*, 3 times at *S* and once at *T*. In only six trials was the orientation clearly effected near the middle of one of the alleys, to which number must be added the number of trials in which immediate orientation occurred. This fact, that the cue is picked up at distinctive positions, cannot be explained on the hypothesis that each rat would finally learn to orient itself at some one of these positions and hence that all of the 15 orientations at *N*, for example, belong to that one rat, as might very well be the case, if such a point offered a distinctive visual or olfactory cue. As a matter of fact, the greatest number of orientations per rat at any position was four out of a total of twelve trials. The 67 trials give an average of 8.37 per rat, and on the average, these 8.37 orientations occurred at 4.75 positions—less than two orientations per position. For any one rat, the greatest average number of orientations per position was 2.2. This general fact that orientation is secured at such distinctive positions as the *turns* supports our general contention.

The statistical results show no differences between the blind and the normal rats in any respect. The females have better records than the males. Their period of exploration is shorter, fewer turns are made inside the alleys, fewer corners are turned, and the percentage of immediate orientations is much higher. Whether this difference is a matter of chance, or whether the results represent individual or sex differences, it is impossible to say.

These various results of the experiment speak for themselves. They can be easily interpreted in terms of our theory. We do not mean to assert that they furnish conclusive and indubitable proof

of our contention, but we do maintain that they can be more readily explained on the basis of our conception⁶ than in terms of a theory which assumes that orientation is secured mainly through some distance sense.

EXPERIMENT II.

THE EFFECT OF SHORTENING AND LENGTHENING CERTAIN ALLEYS IN THE MAZE.

I. The Effect of Shortening the Maze.—For the second experiment, the maze was divided into three sections by sawing it across at the dotted lines. By removing or replacing the middle section, the maze could be shortened or brought back to its original length. This change merely alters the length of four alleys without altering the relation of the turns leading to or from them. The maze was cut very carefully so that the two end sections would fit quite snugly together after the middle section had been removed. For reasons presently made known the cul-de-sac, *B*, remained open during Experiment II.

The trained rats formerly used were employed in this experiment with the exception of the second blind one. This animal became somewhat feeble and refused to work consistently from day to day. After the maze had been sawed through but before the middle section was removed, the animals were allowed to run the maze for seven days. Four trials per day were given each rat. All disturbances of their old habits due to the new smell factors introduced by sectioning of the maze, to the opening of cul-de-sac *B*, and to the tests described above were thus eliminated. After their reactions became thoroughly automatic, the maze was shortened and the behavior of the rats in the new situation was noted. Each rat was given four trials per day for five days.

As above outlined, our theory assumes that the rats make the correct turns in the maze in response to some internal (kinæsthetic) impulse. If the assumption is not true, the rounding of the corners must be in response to some extraorganic stimulation received there. That is, the wall at the end of the runways and the opening into the next alley must contribute data through some distance sense. The experiment is designed to test the relative

⁶ With the exception of the cases of immediate orientation. Since two out of eight animals made eight of the nine unquestioned immediate orientations we are willing to admit the possibility of the use of distance sense data in their cases.

efficiency of these two possible modes of stimulation in determining the rats' behavior at the turns. If the animals run at full speed against the ends of the shortened alleys at *I*, *II*, *IV* and *V*, evidently the assumption that they receive extraorganic stimulation there of functional value to them is most improbable. If the rats succeed in making the turns as correctly as usual, we must conclude that such conduct is determined wholly by extraorganic stimulations and is not influenced effectively by kinæsthetic ones. The experiment is decisive in estimating the relative efficiency of the two possible modes of stimulation, because it brings them into functional opposition.

The results obtained from this experiment justify our assumption that the turns are made in response to differences lying in the kinæsthetic impulses themselves. Marked disturbances of conduct were noticed in every rat. On the average sixteen trials per rat were necessary wholly to eliminate these disturbances, *i. e.*, to secure accurate, automatic adjustment to the shortened maze. Rats can often learn a maze of this complexity *de novo* in this number of trials. This fact is evidence of the profound disturbances effected by the change.

The time for running the maze was increased despite the shortened length. The increase of time was hardly proportionate to the degree of disturbance as reflected in the nature of their behavior. Table I gives the average time in fractions of a minute. The normal time for running the maze in its shortened form was secured by averaging many individual records of trips made after the reactions of the animals had become thoroughly automatic. The records of the seven animals made after the maze was shortened were averaged for each trial. The time increases for the first trials, and then gradually decreases toward the norm.

The disturbances consisted of (1) running squarely into the ends of the alleys at *I*, *II*, *III*, *IV* and *V*; (2) errors, such as partial returns or entering into some of the cul-de-sacs; (3) slow, hesitant and careful movements; (4) stopping here and there and "nosing" around the sides of the alleys, and (5) compensatory adjustments. By the last phrase, we refer to the fact that, after running into the end of an alley for several trials, the rats often attempted to make that turn too soon and would come in contact with the inner corner of the turn. This tendency was most evident at *IV*. The alley *IV* in the shortened maze occupies the

position of cul-de-sac *G* in the lengthened maze. After "bumping" into the wall at *IV* several times, the rats tended to turn too soon and consequently failed to round the turn. As a consequence they formed the habit of running into cul-de-sac *F*. This error was very characteristic and was difficult to eradicate.

TABLE I.

Average time for successive trials in running the shortened maze. (Based upon records of 7 rats).

Normal .21 min.	(5) .33 min.	(10) .25 min.
(1) .39 "	(6) .33 "	(11) .25 "
(2) .45 "	(7) .33 "	(12) .30 "
(3) .45 "	(8) .27 "	(13) .22 "
(4) .37 "	(9) .25 "	(14) .22 "

The following record of Female III, which may be considered typical of the series, furnishes the best description of their behavior.

Sept. 6. (1) Ran into *I* with all her strength. Was badly staggered and did not recover normal conduct until she had gone 9 ft. Ran against *IV* hard and then touched *V* lightly with nose.

(2) Ran into *I* and "nosed" *IV*.

(3) Hesitated at *I* and *IV* but did not touch walls with nose.

(4) Perfect.

Sept. 7. (5) Ran into *I* with sufficient force to land her whole body against the wall. Did not recover normal behavior until after passing *IV*. Stopped at *IV*.

(6) Ran very slowly and hesitantly. Did not gather any momentum. Hesitation at the four crucial corners.

(7) Hugged inner wall at *I*. Stopped at *IV*.

(8) Perfect.

Sept. 8. (9) Slowed up and hesitated at *I* and hugged inner wall at *IV*.

(10) Stopped and "nosed" at *I*, *IV* and *V*.

(11) Perfect.

(12) Perfect.

Sept. 9. (13) Perfect. Ran rapidly.

(14) Perfect.

(15) Entered cul-de-sac *F*.

(16) Perfect.

Sept. 10. All four trials were correct.

One result was obtained which is rather peculiar and is difficult of explanation. The six normal rats found little difficulty with the turn at *II*. Three of these animals effected this turn accurately in every trial. One rat touched the wall lightly on the first trial but made the turn accurately thereafter. The fifth rat struck the wall lightly on the ninth trial, but made the turn perfectly thereafter. The sixth rat hesitated at the turn on the fifth and sixth trials. Out of a total of 120 trials, the rats touched this wall lightly twice, and hesitated momentarily three times. In the remaining 115 cases, the turn was made accurately and unhesitatingly. On the other hand, the blind rat found as much diffi-

culty with this corner as with any of the others. He ran into the wall quite hard the first trial, touched it lightly on the second trial and hesitated there the third trial. On the second day, he ran into the wall twice and made the turn correctly thereafter. It may be supposed that this difference between the conduct of the blind rat and that of the normal rats indicates that the latter effected this turn with the aid of visual data. This assumption is hardly legitimate, inasmuch as the normal animals failed to use vision effectively at the other three corners. Neither can one assume that the turn at *IV* presented visual distinctions not possessed by the other corners, because, if such visual differences exist, they are too minute for the human eye to detect, and, in case the rat possesses a visual acuity superior to that of human beings, it ought to be able to detect a solid wall sufficiently well to refrain from running headlong into it time after time. Again, one may suppose that the normal rats were accustomed to see the opening *B* before reaching the turn at *II*, and made the correct adjustment in response to this visual cue. On this basis, the normal animals should have had no trouble at the turn *V* because the opening *H* bears the same relation to the turn *V* as does *B* to the turn *II*. However, this assumption may be supported by the fact that the cul-de-sac *H* has been open during the previous experiment, while *B* has been open only some eight days. One may argue that the normal rats had neglected the opening *H* as a visual cue in the course of the long series of trials which was given them in the learning maze from the first, while the recent opening of *B* had attracted their "visual attention" and they had learned to utilize it as a visual cue. Such a conception is possible, but the argument is based upon a rather precarious foundation. If the rats can see the opening *B* so as to react to it, it seems that they ought to be able to see the opening into any alley at the turn and utilize it as a visual cue, inasmuch as there is no reason why they should neglect this cue throughout the course of the long series of tests. When the fact was noticed that the normal animals turned the corner *II* correctly, it was suggested that the shortened alley leading up to *II*, which is five feet long, possessed the same kinæsthetic characteristics as some alley in the lengthened maze. As a matter of fact, the alley leading from the box *O*, four and one-half feet long, is very similar to alley *II*. Hence it could be argued that, since the alleys possess the same motor peculiari-

ties, the turns would be made in a similar manner. The conception is ingenious, and it would support our thesis, but on this basis, the blind rat should have had no trouble at *II*. Consequently, we are forced to admit that the phenomenon remains inexplicable so far as the present experiment is concerned.

With the exception noted above, no difference between the behavior of the blind and the normal rats could be detected.

2. *The Effect of Lengthening the Maze.*—After the above series of tests had been completed, the rats were forced to continue running the shortened maze for a period of three weeks, at the end of which time their reactions to it had become thoroughly automatic. The maze was then lengthened by replacing the middle section, and the behavior of the animals under these conditions was observed. In the previous experiment, this middle section had been thoroughly explored by the animals and it should now have presented a minimum of possible sensory disturbance.⁷

The conditions are again such that they bring into functional opposition the influences of kinæsthetic cues and any possible distance sense cues which might be involved in rounding the corners of the alleys. If the rats turn in response to kinæsthetic cues, they should now attempt to turn in the extended alleys at the positions corresponding to the length of the alleys in the shortened form. In the first alley, this position is at *Q'*. In the remaining alleys, the cul-de-sacs *B*, *G* and *H* now occupy these crucial positions. For example, the distance *S-B* in the extended maze equals the distance *S-B'* in the shortened maze. According to our theory, the rats should now run into the wall at *Q'* and into the cul-de-sacs *B*, *G* and *H*.

The results again support our contention. Marked disturbances in conduct occurred for twelve trials (three days). After this time, the disturbances occurred occasionally, though they may be regarded as practically eliminated at the end of this period.

The time for running the maze was noticeably increased in the first trials, but it was gradually decreased thereafter (Table II).

⁷ The blind rat whose behavior had become erratic was not used in the shortened form of the maze. We utilized this animal, however, by allowing him each day to run several times through the lengthened form of the maze. In this way, we kept the middle section constantly in use during the experiments in the shortened maze. By this means, the original smell values of this middle section were retained unaltered, for the males at least, since this blind rat was a male, and was kept in the same living cage with all the other males used in the experiment.

These times, as before, are expressed in fractions of a minute. The normal time was secured by averaging a number of trial records taken immediately before Experiment I was made.

TABLE II.

Average time for running the lengthened form of maze after becoming habituated to shortened form.
(Based upon 7 animals.)

Normal .28 min.	(3) .52 min.	(6) .34 min.
(1) .59 "	(4) .31 "	(7) .35 "
(2) .65 "	(5) .49 "	(8) .34 "

As the best description of their behavior, we give as typical the record of Male I for eight successive trials.

Oct. 2. (1) Came to a full stop at Q' and "nosed" along the wall. Ran into and traversed the full length of alleys B , G and H .

(2) Slowed up at Q' . Entered B its full length. On coming out of B , ran back into A , started from A in the right direction, slowed up at Q' and partly entered B , G and H .

(3) Turned into the wall at Q' and became badly confused. Ran back and forth between Q' and A three times. On coming to Q' the third time, reared upon the wall and "nosed" about. A slight error was made at B . Ran the full length of G and made a slight error at H .

(4) Ran rapidly to Q' and then went slowly until turning the corner. Ran past B but hesitated at G and H .

Oct. 2. (5) "Nosed" along the wall at Q' until turning the corner. Slowed up at B , ran with full speed against the end of G and partially entered H .

(6) Ran past Q' correctly, and went into B its full length. On coming out of B , went back to A , started from A in the right direction, and "nosed" around the wall at Q' , went back again to A , turned and came to Q' and "nosed" about; continued but hesitated at B , G and H but did not enter them.

(7) Slight hesitancy at B and H .

(8) Merely slowed up at Q' , B and H .

All the animals ran into the wall at Q' and into all of the crucial cul-de-sacs. These errors had been eliminated to a great extent by the end of the first four trials (first day's experience), but were again prominent during the first trials of the second and third days. *On entering the crucial cul-de-sacs, the rats frequently ran full speed into the end of the alley.* This is evidence that the cul-de-sacs were mistaken for the true pathway. After a few trials, the cul-de-sacs were entered only part way, and finally the disturbance manifested at these positions consisted of hesitations or of a swerve in the direction of the openings without any decrease in speed. At first, the rats actually attempted to turn through the wall at Q' at the definite position at which they would have had to turn in the shortened maze. Striking the wall at an angle, the rat would slide along it for eight to ten inches and would then go on until it stumbled upon the opening at the end of the alley. This turn occurred relatively accurately (*i. e.*, with respect to old habit) during the first five trials on the average. After this number had

been given, the animal often struck the wall at a point slightly further on between Q' and the corner Q . It seemed that the attempted turn was a resultant of two impulses, one to turn at Q' and the other to go on to Q at the end of the extended alley. Failure to find the opening at Q' often caused the rat to stop and go back in the maze for a new start, or to go ahead slowly until it stumbled upon the opening. In later trials, the animals ran rapidly past Q' without stopping or hesitating, but a *deflection of an inch or two toward Q'* could be noted; the same behavior was noted as the animals passed the crucial cul-de-sacs. In spite of these various disturbances, *i. e.*, hesitations, entering the cul-de-sacs, running into the wall and partial returns over the true pathway, it is a noteworthy fact that very rarely was the confusion so great that the animals ran into any cul-de-sac other than the three crucial ones.

No differences between the behavior of the normal animals and that of the blind rat could be detected.

The results of these two experiments, combined with those reported in the previous paper, form rather conclusive proof of the contention as to the fundamental importance of the kinæsthetic factor in the rat's adjustment to the maze.

CONCLUSION.

In concluding this paper, it may be well to reformulate our contention even at the expense of repetition, by contrasting the habits of the rats in the maze with the habits of human beings in a similar environment.

Human beings can form habits of the type we have been discussing (kinæsthetic-motor) which may become absolutely automatic. When this latter stage has been reached the "movement to come" is released at the proper time by the afferent (kinæsthetic) impulses aroused by the movement which has just been made. So far, these statements apply alike to the behavior of rat and man.

When an automatic series of movements in man is disturbed, the "movement to come" can no longer be released by the afferent impulses arising from the movement just effected. Visual, auditory or tactual impulses (cues) are then utilized, *i. e.*, the adjustment becomes, *e. g.*, momentarily visual-motor. A few move-

ments made in response to these distance sense cues may suffice to restore the kinæsthetic-motor character of all the ensuing adjustments.

Likewise, when an automatic series of acts in the rat is disturbed, the "movement to come" can no longer be released by impulses arising from the movement just preceding. But at this point the analogy between the behavior of rat and man breaks down. The former apparently has no well developed distance sense cues, consequently he must utilize some method other than the one above described to reestablish the automatic character of his acts. Our hypothesis provides the rat with such a method. According to it, the rat has the possibility of receiving kinæsthetic cues which function for "control" exactly as do visual cues in man. These kinæsthetic cues are ordinarily not needed by the rat for controlling his movements any more than visual cues are needed by man for controlling his. But the moment a break occurs in the series of the acts of the rat a cue is needed which will lead to the reestablishment of the automatic character of the movement. The rat receives this cue by traversing at random any "unit" of the maze. The group of afferent impulses (kinæsthetic) which are aroused by traversing this unit releases the proper adjustment (*i. e.*, the old movement which has been synergized on many past occasions with this particular group of impulses) and the automatic character of the movements is again restored.

On this supposition, man's kinæsthetic-motor habits would differ from the rat's mainly in this, that whereas the former utilizes distance sense cues for reestablishing automatic adjustments, the latter utilizes kinæsthetic cues.

STUDIES ON NERVE CELLS.

I. THE MOLLUSCAN NERVE CELL, TOGETHER WITH SUMMARIES OF RECENT LITERATURE ON THE CYTOLOGY OF INVERTEBRATE NERVE CELLS.

BY

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WITH PLATE I AND THIRTEEN FIGURES IN THE TEXT.

I. INTRODUCTION	45
II. MORPHOLOGY OF THE GASTEROPOD NERVOUS SYSTEM.....	48
III. LYMPH CANALS.....	50
IV. VACUOLES	55
V. THE NISSL BODIES.....	61
VI. PIGMENT	69
VII. THE CENTROSOME IN NERVE CELLS.....	73
SUMMARY	75
LITERATURE	76

I. INTRODUCTION.

The purpose of this paper is twofold: First, to summarize and correlate the more important contributions on the structure of invertebrate nerve cells exclusive of the neuro-fibrillæ (a special problem which cannot be adequately treated in the space allotted to this review); and, second, to present our own studies on the structure of the gasteropod nerve cell with special reference to the problem of the so-called NISSL bodies, whose nature is still in controversy. It has been maintained that these bodies are artefacts. Inasmuch as we have been able to cause them to appear by feeding experiments and have been able to photograph them in the living and unstained nerve cells, we feel reasonably sure of their actual existence and shall make suggestions as to the manner of their development, as well as their probable function. In a

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later paper we hope to show structural and physiological similarities between the nerve cells of invertebrates and vertebrates.

The various terms employed to describe the stainable and non-stainable substances of the cytoplasm of vertebrate nerve cells have been in large measure carried over to the description of the invertebrate nerve cells. Since the NISSL bodies were discovered and known as the visible or stainable part of the cytoplasm, the following words have been used for similar structures; the chromatic substance, the chromophile part of the cytoplasm, the chromatophile elements, the chromophilic particles, the basophile constituents, the tigroid substance, the sigroid substance, the collagenous substance, granules or granular substance. The names of most of the authors who have created this confusing and unnecessary terminology may be found in ROBERTSON'S review. In a similar manner the non-stainable substance is designated as the achromatic, fundamental, invisible, not formed, unstainable, acidophile substance, trophoplasm, or kinetoplasm. The fibrillar substance is included in these terms although it is a distinct structure and whether it is considered as a part of the stainable or non-stainable substance depends largely on the writer.

The pigment found in nerve cells of the central nervous system is deposited in masses distinct from the NISSL bodies and is pale yellow or dark brown. These seem to be unlike, the brown appearing early in life and ceasing to increase after a few years. It is not blackened by osmic acid. The yellow appears in man during the sixth year, increases with age and is blackened by osmic acid. Some writers maintain that the yellow is not fat, but that it undergoes fatty degeneration. In certain mental diseases there is an accumulation of this pigment and a breaking down of the structure of the cytoplasm. Whether the two processes are related or not is unknown. A golden yellow pigment is found in the nervous system of certain gasteropods and a yellow pigment in other classes of invertebrates, the origin and use of which are somewhat problematic.

A further modification of the cytoplasm of nerve cells is found in the presence of vacuoles, lymph spaces and the actual though infrequent penetration of nerve cells by capillaries. The vacuoles occur in the cytoplasm, nucleus, and nucleolus and are probably in each case formed in a similar manner even when the exciting cause is different. The vacuoles which occur in the nucleolus

are similar to those that occur in this structure in ova in most animals during their growth. The vacuoles that occur in the nucleus are not as common and it is doubtful whether they are normally present. So far as we are aware they have not been seen in the living nerve cells, but are common in cadaveric specimens. Nerve tissue poorly fixed may also exhibit them, which renders it all the more probable that they are artefacts.

The vacuoles in the cytoplasm are present in the nerve cells of many animals both vertebrate and invertebrate. *They can be seen in the living nerve cells of Gasteropods* and have been reported in some vertebrate nerve cells. In well fixed and stained sections, vacuoles are very commonly found which agree in form and appearance with the conditions in the living cells. Considerable work has been done to determine the question whether or not these cytoplasmic vacuoles have a definite wall. It is necessary in this connection to distinguish the vacuoles from the lymph spaces and capillaries. The vacuoles are usually small and irregularly distributed throughout the cytoplasm. They contain a homogenous fluid or differential bodies, and their presence is, we believe, intimately associated with the metabolism of the cell and probably with its constructive phases. These vacuoles vary in number in the same animal and in the same species. This would indicate that they are transitory structures which appear when certain chemical changes occur, and then disappear. A very critical study of the cytoplasm in contact with the vacuoles fails to show any evidence of a separate wall. The vacuole in the living nerve cell forcibly reminds one of the food vacuoles in protozoa which appear to have a wall; but this appearance is really due to the contact of fluids of different refractive index. In stained specimens the vacuoles look as if they were limited by a more deeply staining border, but this may be explained as due to the accumulation of cytoplasmic granules about the enclosed liquid. We believe that it is no more proper to speak of a wall for these vacuoles than it is to say that the numerous vacuoles in a protozoan have walls.

The lymph spaces are of a different character and are usually located in the periphery of the cytoplasm. They are intimately associated with the circulatory system and may contain blood. In some of the larger invertebrate nerve cells the periphery is richly supplied with lymph canals which may occasionally contain corpuscles. These canals or spaces can in many instances

be traced directly into the surrounding neuroglia tissue and appear to be of a more permanent character than the vacuoles. We are inclined to believe that these lymph canals are supplied with definite walls.

A sufficient number of cases has been described to show that occasionally nerve cells are actually penetrated by capillaries. We have observed one instance in *Helix*. These capillaries terminate in finger-like branches or pass through the cell or even through two or three adjacent cells. They have a definite wall and contain blood corpuscles.

The question as to how the nerve cell is nourished, and how it maintains itself during long periods of excitation, long fasts or hibernation is one which has attracted the attention of scientists and will continue to do so. The appearance and disappearance of the granular particles in the cells at once gives evidence that they are temporary structures. It is natural to think of nerve cells as performing *one* function, and we frequently lose sight of the fact that the cell has a protoplasmic structure which must be nourished just as truly as that of any other cell. The activities of a nerve cell are not all of a nervous character; metabolic processes must go on here just as truly as in the muscle cell or the gland cell. But these processes may be overshadowed or concealed by the more specialized activities of the cell.

We shall attempt to show that these metabolic processes actually take place within the nerve cell, that certain food substances are stored up within the nerve cell, that these substances may remain in the cells for long periods, and that they may be called upon at any time of want or stress to supply material out of which new protoplasm may be built or to act as a source of energy.

Twenty years after the admirable work of NANSEN, we can do no better than to quote from him the following sentence. "If we look through the modern literature having special reference to the invertebrate nervous system, and compare the many different views of the structure of the ganglion cells, we meet with a confusion on the subject which is far from encouraging."

II. MORPHOLOGY OF THE GASTEROPOD NERVOUS SYSTEM.

Much of the work on nerve cells where a direct stimulation has been employed has been on a certain ganglion through a specific

nerve passing to that ganglion. The nervous system of gastropods does not permit of any such treatment, as the following description and diagram shows. The nervous system of *Limax* may be taken as typical of the common snails. It makes its first appearance on the sixth or seventh day after the eggs are laid (HENCHMAN '90) and is derived entirely from the ectoderm. The several ganglia which constitute the nervous system of *Limax* arise separately to become secondarily joined by commissures.

In the adult stage, the central nervous system consists of five pairs of ganglia and a single ganglion asymmetrically placed. The relative position of the ganglia can be appreciated from the view shown in Fig. 1. "In passing from behind forward, the ganglia are encountered in the following order: (1) The pair of pedal ganglia, which lie under the radular sac, and are joined to each other by an anterior and a posterior commissure; (2) one abdominal ganglion a little to the right of the median plane (which is intimately fused with the right visceral, and is also in close connection with the left visceral ganglion, p. 199); (3) a pair of visceral ganglia occupying the posterior angle formed by the outgrowth of the radular sac from the œsophagus. They are

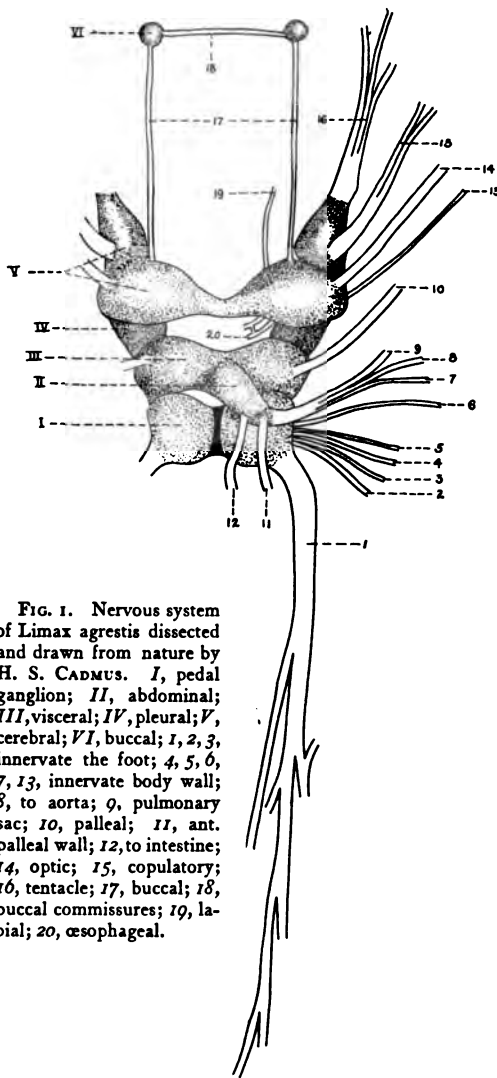


FIG. 1. Nervous system of *Limax agrestis* dissected and drawn from nature by H. S. CADMUS. I, pedal ganglion; II, abdominal; III, visceral; IV, pleural; V, cerebral; VI, buccal; 1, 2, 3, innervate the foot; 4, 5, 6, 7, 13, innervate body wall; 8, to aorta; 9, pulmonary sac; 10, palpal; 11, ant. palpal wall; 12, to intestine; 14, optic; 15, copulatory; 16, tentacle; 17, buccal; 18, buccal commissures; 19, labial; 20, œsophageal.

separated by the abdominal ganglia from which connectives pass to them; (4) a pair of pleural ganglia, not joined by a commissure and not giving off nerves. They are united by means of connectives to the pedal, visceral, and cerebral ganglia of the same side; (5) a pair of cerebral ganglia with their supra-oesophageal commissure and connectives to the pleural, pedal, and buccal ganglia; (6) a pair of buccal ganglia, with a commissure under the oesophagus posterior to its connection with the sac of the radula." (Quoted from HENCHMAN '90, p. 193.)

A comparison of this drawing with those of pond snails by LACAZE-DUTHIERS shows a number of differences in respect to the origin of the nerves and the announcement of two nerves that are not shown in his figures.

III. LYMPH CANALS.

Structures known as lymph canals we differentiate from vacuoles, although both have a similar appearance in the fixed cell. This distinction is made after a study of the living nerve cell. In a subsequent section on vacuoles it is suggested that in certain instances the lymph canal, trophospongium, etc., are not real lymph spaces, but isolated and independent vacuoles. That lymph canals do really exist in nerve cells seems to be well established, as the accompanying review indicates. Our study of fixed material in *Helix* and *Aplysia* shows that the outer border of the cytoplasm is frequently penetrated by spaces, as well as numerous processes from the neuroglia. Many of the drawings of RHODE and HOLMGREN indicate a similar state of the cytoplasm so that we believe that these lymph canals have a rather general distribution in invertebrate nerve cells. HOLMGREN in his several papers has given an elaborate account of lymph-spaces. Apparently the same class of structures had been previously described under the caption "intercellular neuroglia" by RHODE. RHODE observed these structures in various animal classes, making a special study of *Aplysia*, *Helix*, and *Doris*. His results are interpreted in terms of his theory of work on the part of the neuroglia cells. The neuroglia cells are not considered as intruders but as cells which by their activity build up the nerve cell.

In order to give some conception of the extent and importance of the work on lymph canals, the following rather full review is made.

Our review of the work of HOLMGREN can give us at best but an inadequate conception of its amount and quality. His numerous papers, while somewhat controversial, contain a large range of observations on *fixed* nerve cells, both vertebrate and invertebrate. His main contention seems to be centered around the character of the cytoplasm. Whence come the numerous spaces in it, and what of their character? It seems to us necessary to include here a review of some of his studies upon the nerve cells of vertebrates, since he makes this his starting point. A good summary of HOLMGREN's ideas concerning the structure of the nerve cell may be found in vol. II of MERKEL and BONNET's *Ergebnisse*.

HOLMGREN ('01) makes the first mention of the "Saftkanälchen" in the spinal nerve cells in his paper on *Lophius piscatorius*, where he makes the following statement, "localized endocellular nets of 'Saftkanälchen' are seen especially well in the rabbit." A thick network of fine tubules is to be seen in the cytoplasm surrounding the nucleus, and usually near the poles of the cell. The sectioned lumina of the tubules are always circular in outline and are always sharply marked off. Here and there one can find how these networks of tubes are connected with the pericellular tubes. In these places the walls are clearly marked. Within the cells the author could see no definite walls to the canals. Most of the cells of the spinal ganglia possess such networks, but they do not always seem to agree with each other with respect to the breadth of the lumen or the wall of the canal.

In the cells the author distinguishes two cytoplasmic zones, an inner canalicular and an outer extra-canalicular zone. These canals are supposed to have walls—at any rate something which appeared to be a wall stained red with erythrosin. In addition to the observations just cited upon the rabbit, the author studied the dog, cat and various birds. In these animals he found remarkably strong dilated canals winding in a corkscrew manner through the ganglion cells. From the perior extra-cellular tubes more or less numerous canals force their way into the ganglion cells. Inside of the cell they often divide in the characteristic finger-form manner, and they turn in manifold ways, not infrequently in spirals. By this means there exist glomerulus-like collections of tubes in the cell. In the case of the birds there were seen canals so strongly dilated that the protoplasm appears only as islands or thread-like heaps between the tubes. These dilations or tubes are not localized in any particular part of the cell but may be found in any part. He says that these tubes must correspond to the bands which were described by NELIS, with the exception that NELIS did not make any mention of bands going out of the cell. Such connections do not exist in all cases, but are nevertheless general. HOLMGREN could find these cells in the sympathetic and central nervous system of birds. He considered the canals which may be continued beyond the limits of the nerve cell as lymphatic passages.

As opposed to STUDNICKA, HOLMGREN says that the lymph canals come from the anastomosis of vacuoles or alveoli, and again he states that the canals in the case of *Petromyzon* are bounded by intensely staining walls which continued rectly outside of the nerve cell into the walls of the extracellular paths.

If one stimulates the spinal ganglion cells by means of weak induction currents, almost all parts of the whole canal are strongly widened. This agrees with the statement of NELIS that the bands occur in altered cells. "The nerve cells are permeated with a very rich canal system hitherto unsuspected, and only the more dilated parts of these networks are the passages which I was able to see before."

The great dilations of the canals are certainly only accidental, and so one can understand without anything further the great variability of the canals.

After working upon a variety of animal forms both vertebrate and invertebrate, and especially upon *Lophius*, the author concludes that his former position in harmony with that of FRITSCH ('86) is a mistaken one and that the vessels are not blood vessels within the nerve cells but are to be considered as lymphatic in their nature, and that they press their way into the nerve cells and there branch about. Among the invertebrates he finds *Astacus* and *Palæmon*, next to *Lophius*, excellent material for clearing up the true nature of the lymph canals.

In very young animals he finds the canal net to be remarkably simpler than in the case of older animals. Often this net is to be found at one pole of the very eccentric nucleus. The sympathetic nerve cells of the mammals show the canal nets only within the cell body. The same nerve cells of the bird, like the central nerve cells of all the vertebrates studied, possess continuations of the net also within the dendrites. An electrically stimulated nerve cell of the bird will show, according to HOLMGREN, the presence of the lymph canals in the neurites.

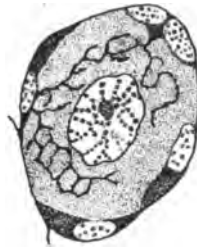


FIG. 2. The intracapsular cells surround the nerve cell. The trophospongium branches as a net of coarse threads through the endoplasm and at two points reaches the surface connecting itself with the colored bodies of the intracapsular cells. After HOLMGREN ('04, Fig. 1).

The question as to the morphological and genetic character of the lymph canals has been much discussed and various opinions held. NELIS considered them as achromatic hyaline bands, but he seems to be somewhat uncertain in his meaning. To him they are riddles as to morphology and function. HOLMGREN and his followers believe them to be canal-like, fluid carrying structures. According to HOLMGREN and his followers the bands of NELIS are only modified parts of the lymph-canals. HOLMGREN opposes the view that they are formed out of the nerve cells but holds that they press into the substance of the nerve cells from without in the form of hollow processes (*Kapselfortsätze*). He further claims to have seen unmistakable nuclei-bearing capsule processes in the spinal nerve cells of *Lophius* and other teleosts, also in the gastric ganglion cells of the Crustacea, within which there were sap spaces. According to his view these canals do not represent drainage tubes but are rather the morphological expression of certain phases of the penetration of nerve cells and the intracapsular cells belonging to them. The trophospongium has pseudopodia-like mobility whose intensity is supposed to depend upon intracellular chemical processes (Fig. 2).

The lymph-canals are of a lymphatic nature and are certainly associated with

the nourishment of the cell. NELIS claims that as the nerve cells change there is a decrease of the tigroid substance which is accompanied with an increase in the amount of the transparent bands. HOLMGREN believes that the localization of the tigroid substances should coincide with the appearance of the canals, that the canalicular zone of the cell should be the tigroid layer free of ectoplasm. The tigroid substance stands in a causal relation to the lymph clefts and is associated with their activities. Where the clefts are especially dilated, a rich accumulation of tigroid substance takes place. In more protracted periods of activity the clefts become smaller and the tigroid substance vanishes; but in such places where the tigroid substance remains, the clefts remain dilated. Electric stimulation points to the same conclusion. The nerve cells, as a result of such a stimulus, receive new supplies of tigroid substance and at the same time become somewhat larger; accompanying this, there is a dilation of the lymph clefts. This leads one to believe that the electric current calls forth an alteration of the circulatory relations. HOLMGREN cites a number of investigators whose work bears directly on the interpretation of these structures as follows:

ADAMKIEWICZ ('86) from his researches with injections could have made the same report, that the nerve cells are furnished with their own blood vessels and that the nuclei of these cells should present venous spaces, but these discoveries have nothing to do with the sap canals which do not carry blood. From the work of other investigators it is evident that blood vessels very rarely enter nerve cells.

FRITSCH ('86) found that blood vessels were constantly to be found in the giant ganglion cells of *Lophius piscatorius*. HOLMGREN uses the results of FRITSCH to confirm his own belief that lymph spaces exist in the cell, but makes the additional statement that the blood capillaries are supposed to be drawn into the cell through endocellular branching processes. In 1900 HOLMGREN came to the conclusion that these spaces in the cells were not to be considered as blood vessels but rather as lymph spaces in so much as they do not carry corpuscles. STUDNICKA in the same year expressed the same belief, though more indirectly.

NELIS ('99) describes in nerve cells homogeneous non-staining bands of a skein-like appearance found within the cell. These appear in various places in the cell body. They exhibit various forms, half moon, spiral, corkscrew, and hang together at the ends, but do not form a true reticulum. They are to be found in the cells of the spinal and sympathetic systems as well as in the brain. They are particularly prominent in animals which have been poisoned. HOLMGREN claims that these structures are the same as are called "Saftkanälchen."

STUDNICKA ('99) held that the canals are formed from the running together of vacuoles which had formed in the cell in a row.

BETHE ('00) opposes this view on account of the fact that he had observed single canals which passed completely through several nerve cells and their capsules at the same time.

FRAGNITO ('00) regarded the canals as the remains of the interstices between the neuroblasts, through whose melting together the single nerve cells are supposed to come into existence.

PUGNAT ('97) believes that the canals force their way into the nerve cells from without, as lymph capillaries.

PEWSNER-NEUFELD ('03) studied the finer anatomy of the nerve cells in the nervous system of the white rat and guinea pig. He does not find that there are

distinct zones in the plasma of the cell. Small canals are scattered throughout the cytoplasm, no region being free from them. They do exist in the nucleus (Fig. 3). The canals may or may not occur in the protoplasmic processes of the cell. The canals run about the Nissl flakes, sometimes passing through them, at other times merely surrounding the flakes, or they may be free in the cytoplasm. Some of the small canals approach the nuclear membrane, but in no place were they seen to penetrate it. The size and extent of the canals is dependent on the physiological state of the cell. The canals do not have a distinct wall but a linear boundary due to the arrangement of the cytoplasmic granules. The intracellular lymph canals of the central ganglion cells open into channel-like spaces.

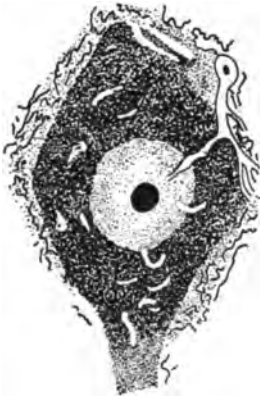


FIG. 3.

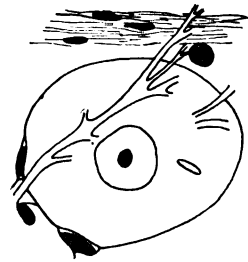


FIG. 4.

FIG. 3. Ganglion cell of white rat. Illustrates penetration of cytoplasm and nucleus of nerve cell by sap canals. The isolated clear spaces are the cut ends of sap canals. After PEWSNER-NEUFELD ('03, Fig. 3).

FIG. 4. A large ganglion cell with tubes formed from the capsule extending entirely through it. After BETHE ('00, Fig. 2).

STUDNICKA ('99) presents a discussion of the origin and use of the canals in ganglion cells. The little canals can very often be followed in the body of the cell some distance, indeed, often through the half of the entire cross section of the cell. They are seen in such a study to branch freely. These little canals which are identical with those described by HOLMGREN, arise very likely through the union of a row of vacuoles. Many of the canals have smooth outside walls. Some separate vacuoles are found which are explained as being the cross sections of the branches of such vacuoles as have not yet fused into canals. He is unable to define the contents of the canals and alveoli, but suggests that they are during life, no doubt filled with a fluid which may be identical with that in the pericellular space with which the little canals are united. Some of the greater alveoli contain a homogeneous substance which colors more intensely with eosin and is to be considered a special deposit.

BETHE ('00). We have here to do only with dependent canals (blood vessels) which can be proven only by injections. No nuclei are to be found in the walls of these canals. The canals result from the fusion of separate vacuoles. The canals have nothing in common with the neuro-fibrillæ (Fig. 4).

IV. VACUOLES.

The presence of vacuoles or vacuolar-like structures in the cytoplasm of nerve cells is a common structural character. They have been recorded as follows:

HODGE's ('92, '94) work is of great importance to all interested in the question of fatigue and the accompanying structural changes in the nerve cells. The spinal ganglion cells of the frog, cat and dog, under electrical stimulation and the spinal ganglion and brain cells of English sparrow, pigeon and swallow show the following changes. The nucleus undergoes a marked decrease in size and changes from a smooth and rounded structure to one having a ragged outline. Its reticulate appearance is changed and the whole structure takes a denser stain. The cell protoplasm gives evidence of slight shrinkage and the formation of vacuoles. These vacuoles appear quite constantly in the ganglion cells of birds. The vacuoles have a sharp outline and a definite shape in the rested animal but are indistinct in the bird that has been at work during the day. Vacuoles also appear in the honey bee under the following conditions. Honey bees were collected in a raspberry patch as soon as they appeared in the morning. The first six bees were quickly decapitated, the brains removed, and three were dropped into one-half per cent osmic acid, and three into saturated mercuric chloride solution. At about seven o'clock at night six more bees were captured and treated in the same manner. After the morning and evening bees had been paired at random, each pair was stained and studied and an attempt was made to measure the nuclei and work out the amount of shrinkage. The minimal shrinkage was 9 per cent, and the maximal 75 per cent. The author does not attach much value to these figures, although they express the fact that a wide difference exists between the two. The average in diameter of the morning bees is more uniform than for the evening bees. These results indicate first, that the nerve cells of a number of bees' brains are in a more uniform condition in the morning than in the evening. Secondly, they differ in appearance, or condition, from one another, somewhat in the morning and a great deal in the evening.

MONTGOMERY (97) finds in the nemerteans, *Cerebratulus* and *Lineus*, chromophilic corpuscles under the following conditions: The cytoplasm of the medium sized cells is of a coarsely vacuolar structure; sometimes the hyaloplasm fills the whole proximal portion of the cell as far as the nucleus. But a thin, peripheral layer of spongioplasm is always present, and a similar layer envelops the nucleus. These cells are much larger in *Cerebratulus* and the cytoplasm is much denser, *i. e.*, there is a proportionately greater amount of spongioplasm, and a coarsely vacuolar structure is seldom found. The large cells of the brain are of an elongated pyriform shape, largest and rounded proximally, seldom nearly spherical. It may be noted that while the cell bodies vary considerably in size, their nuclei remain of nearly uniform dimensions. The cytoplasm is, as a rule, coarsely vacuolar

(vesicular), especially so toward the distal pole. A thin peripheral layer of finely granular cytoplasm is always present. The vacuoles do not seem to have any definite grouping, but such groupings as exist are explained as corresponding to the different physiological states.

Certain bodies occur in these ganglion cells in *Lineus* which are absent in all of the cells in *Cerebratulus*. These bodies are frequently larger than the nucleolus and of a spherical or oval shape, and are not refractive. After the use of a double stain they stain usually with eosin, sometimes with hæmatoxylin, but always more intensely than the surrounding cytoplasm, though seldom as deeply as the nucleolus. Structurally, they are homogeneous, with a peripheral membrane, which may be scarcely discernible or in other cases, of considerable thickness; this membrane always stains more intensely than the enclosed portion, and forms a boundary against the surrounding cytoplasm (Fig. 5). These bodies do not occur in all cells, but only in about one-sixth of the total number; when they are present, it may be but a single one, more frequently four or five, apparently never more than



FIG. 5.



FIG. 6.

FIG. 5. *Lineus gessnerensis*. Ganglion cell of the third class, showing the presence of vacuoles, some of which contain differentiated granules. After MONTGOMERY ('97, Fig. 9).

FIG. 6. *Nereis*, brain cell of sixth class. Nucleus lies in narrow end surrounded by granular cytoplasm, while in the other end there is a large vacuolar space. After HAMAKER ('93, Fig. 17).

fifteen. There is also no regularity in their distribution, such as a concentric or radial arrangement, and in the same cell they are usually of various sizes and of different staining power. To these cytoplasmic bodies may be applied the term chromophilic corpuscles, to distinguish them from the chromophilic granules in the ganglion cells of other animals.

RAND ('01) reports vacuoles and gives an analysis of the cytoplasm as follows: Very little can be said as to the finer structure of the cell protoplasm in the *Lumbricidæ*. The most careful examination fails to reveal its precise nature. It varies in degrees of homogeneity somewhat according to the size of the cell. In the smaller cells, it usually appears compact and fairly homogeneous. In larger cells, it is much less homogeneous, and there is a tendency toward the formation of large vacuolar spaces. The substance of the fixed cytoplasm, as it appears to the eye, may be said to be of four kinds. There is (1) a perfectly homogenous "ground," represented by the lightest areas in the figures; (2) material which gives the impression of being very finely granular; in the smaller cells this is quite evenly

distributed, while in the larger cells it tends to concentrate in regions, giving the cytoplasm a blotchy appearance; (3) rather conspicuous granules or masses staining fairly deeply and often surrounded by an area within which the material of the second class is less dense; (4) a fine fiber irregularly distributed through the cell body, but often appearing to be associated with the more conspicuous granules and sometimes occurring about granules as centers of radiations.

HAMAKER ('93) shows in one type of the nerve cells in *Nereis* the following: In the posterior half of the brain there are several pairs of very large cells which have a very striking characteristic. The nucleus lies in the narrow end of the cell, and is surrounded by the granular cytoplasm. At the other end of the cell, there is a large vacuolar space containing a number of deeply staining bodies of irregular form, embedded in an indistinct coagulum (Fig. 6). Other cells have very finely granular substance occupying a similar position, the granules being much smaller and staining less deeply than those of the body of the cell. In these cases the nucleus shows no signs of degeneration.

LENGENDRE ('05, '06) in a series of short papers during the years 1905 and 1906 has given us reports of an investigation on nerve cells of Gasteropods. He has studied the cell from the physiological point of view, with the idea of determining whether the structures described by HOLMGREN and others are in any way related to the nutritive functions of the cell. He follows the work of HOLMGREN, BOCHENEK, MCCLURE, RHODE, and others. A study is made of the effects of various fixing reagents and he finds that RABL's solution is a very poor reagent for the study of nerve cells. Consequently many of the results which have been obtained through the use of this fluid are to be considered as artefacts and not as actual structures which exist in the living cell. He questions the work of RHODE and does not believe that the fibrils of the nerve protoplasm are continuations of the processes of the neuroglia cells on account of the difference in size and staining qualities. He finds in the cells of *Helix pomatia* vacuoles of various sizes, arranged in various ways in the cell. Sometimes they communicate with one another and sometimes open to the outside of the cell. These vacuoles are without definite walls and contain a homogeneous fluid without granules. The chromophile granules are always found in the protoplasm when present at all and never appear in the vacuoles. LEGENDRE does not admit the theories of HOLMGREN concerning the nutritive functions of the nerve cells. He advocates in his first paper that the vacuoles represent accumulations of excretory products and that they are in no way connected with the constructive metabolism of the cell (Fig. 7).

In these papers he calls attention to the following points: He describes the appearance of living nerve cells that have been immersed in water for a considerable time. The result is a rapid increase in size due to osmotic exchange. In the protoplasm of the cells thus treated the meshes of the spongoplasmic net become greatly enlarged and more clearly visible. The nucleus becomes large and numerous vacuoles appear in the periphery of the cytoplasm. He also advances the idea that the HOLMGREN canals in the trophospongium are to be interpreted as pathological rather than nutritive and that they act more like the phagocytes in that they destroy cell substance rather than build it up.

PFLÜCKE ('95) notes the presence of a few vacuoles in the cell plasma which he does not regard as true vacuoles but as accumulations of unstainable substance.

EWING ('98) takes an extreme position in regard to the presence of vacuoles, claiming in the majority of cases that they are cadaveric or artificial products.

The formation of vacuoles has long been recognized as one of the necessary imperfections in most methods of fixing of nerve cells. The writer cannot agree with the statement often seen that the vacuolation may be regarded as pathological only when it is found in advanced degree. Among the present cases, extreme vacuolation when found, was always plainly referable to post-mortem processes. The study of cadaveric changes in ganglion cells indicates that vacuoles are one of the most constant of post-mortem products; and that they frequently form in considerable numbers and of large size within a few hours, often preceding other post-mortem changes. Especially when the brain and meninges are œdematous, or when the patient has suffered from general sepsis, vacuolation of cells may be expected unless the tissues are fixed very shortly (one half hour) after death. The above observations, as well as the circumstances under which vacuoles are usually found in stained specimens, indicate that in the great majority of instances vacuola-



FIG. 7.

FIG. 7. *Arion rufus*. Vacuolated condition of cytoplasm and granules in the axone hillock. After LEGENDRE ('05, Fig. 1).

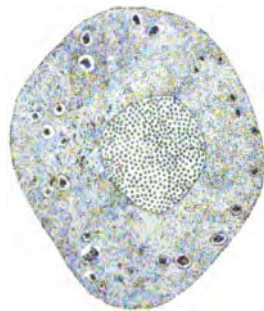


FIG. 8.

FIG. 8. Ganglion cell of *Tethys* with a number of mitochondrien masses either in clear spaces limited by a definite wall or free in the cytoplasm. After RHODE ('04a, Fig. 10).

tion of ganglion cells is a cadaveric or artificial product, and in any case with the present state of our knowledge, is devoid of definite pathological significance. It is doubtful if the structures known as nucleolar vacuoles are to be regarded as of a similar character with the vacuoles of the cytoplasm.

RHODE presents numerous facts in his several papers in regard to the structure of the ganglion cell. The sphere referred to in the following is a differentiation of the cytoplasm of a distinct character and should not be confused with the sphere associated with the centrosome. According to RHODE ('04a) the sphere in the ganglion cell of *Tethys* consists of a central part surrounded by a clear layer having the granules arranged compactly and in a radial manner. The clear layer is made up of a homogenous or fine granular substance which colors intensely (Fig. 8). The outermost bodies in the peripheral layer of granules may fuse completely so

that there is the appearance of a thick membrane which seems to separate the sphere from the cytoplasm. The clear region may be encroached upon and occupied by radially arranged granules which vary in size. All stages in the origin of the sphere may easily be seen in the same ganglion cell. In the frog these same spheres have a nuclear origin, *i. e.*, they are derived from the smallest bodies in the nucleus. In the same manner as in the frog, arise the spheres in *Tethys* with this difference, that the origin does not take place within, but without the nucleus. The various stages in the development of the spheres are seen in the cytoplasm, which may be compared to similar stages in the development of the spheres in the ganglion cells of the frog.

When the spheres attain a certain size, their destruction occurs as follows: The central body becomes indistinct and the radial zone breaks up into large or small pieces, finally becoming so small that they cannot be distinguished from the cytoplasmic granules so far as their shape is concerned, but they retain their avidity for stain, which gives them prominence everywhere. Some of the large spheres do not go through these regular changes and are described as vacuoles (*Bläschen*) with a thin wall and a clear center. In the transformation of the sphere into a vacuole this stage corresponds to the term "*Mitochondrien*." When the peripheral layer of the sphere is broken up into a number of loose threads the term "*Chondromiten*" is applied to them. The largest spheres are as a rule the oldest and arise out of the smallest, structureless globules (*Kügelchen*) of the cytoplasm. These may be seen to grow and to differentiate themselves into a light inner zone and a dark outer band. The larger the sphere, the more plainly the granules, which finally assume a radial arrangement in the outer zone, appear. The last stage in the formation of the sphere shows the central body assuming its complete shape and size.

SMALLWOOD ('06) reported the presence of numerous vacuoles in *Haminea*, *Venus*, *Planorbis*, *Limax*, *Helix*, *Littorina*, *Melantho*, *Montagua* and *Aplysia* which were designated as lymph spaces. A more extended study suggests that this term should be reserved for the larger peripheral spaces and that the term vacuoles more correctly describes them. There is no definiteness about their position or size in the cell (Fig. 7). Animals examined during all seasons of the year show them to be present in living nerve cells.

From this review, we learn that the nerve cells of Nemerteans, Annelida, Crustacea, Insecta and Mollusca among invertebrates exhibit a highly modified cytoplasm. A sufficient number of specimens have been examined in each of these great groups to indicate the very general appearance of differential structures in the cytoplasm other than fibrillar. In the introduction eleven different terms are cited as having been given to this stainable substance in the cytoplasm which of itself suggests that the problem is one of great difficulty; certainly a doubt must have existed

in the minds of the various workers who have coined these terms as to their significance and relationship.

It is rather hard to make a classification of these structures as described by the various authors because in most instances the cytological study was not followed or preceded by an examination of living nerve cells. Our results have been so clear and satisfactory that we are tempted to try to correlate some of the previous facts with them. Probably the commonest structure present in the cytoplasm of the invertebrate nerve cells is the *vacuole*. These vacuoles are present in all of the great groups already cited, although usually described under the terms "lymph space," "Netzapparate," "Saftkanälchen," "Trophospongien," etc. The vacuole can be determined in the following manner in the living cell: Isolate a nerve cell and study it in a 1-500 solution of methylene blue or neutral red in normal salt solution under the oil immersion lens. At first, but little can be determined; but as the stain progresses the vacuoles become more distinct and their contents often take on a differential stain. The experienced worker can make out these vacuoles without any stain. The time that it takes to stain these vacuoles will vary; but usually from 5 to 20 minutes will be the limit, as after that time the nerve cell is apt to become overstained and undergo some changes in its general appearance and the character of its parts. This gives about 15 minutes when a critical study may be made. During this time the vacuoles are readily made out as isolated spherical bodies containing a fluid. It is impossible to trace any connection between vacuole and vacuole. The size is also further evidence of their individuality, for they range from the very minutest bodies recognizable with the oil immersion lens to structures a third the size of the nucleus. Studying these vacuoles in *Planorbis* and *Limax* for two years, in which we examined almost weekly the living nerve cells from hundreds of specimens, we are convinced that these vacuoles are transitory structures, that they vary in number from time to time, and that they are not limited by a distinct wall. The vacuoles move about in the cytoplasm when the nerve cell is put under pressure, which would be impossible if they were part of lymph spaces that had grown in from the surrounding neuroglia tissue.

The Chronodromiten and Mitochondrien of RHODE, the Trophospongien of HOLMGREN as interpreted by BERGEN, present in *Helix* but not figured by McCLURE, the chromophilic corpuscles

of MONTGOMERY, the vacuolar spaces of HAMAKER, the granules within clear spaces of RAND, the numerous vacuoles described in *Arion* by LEGENDRE, all, we believe, are to be classified as nerve cell vacuoles. The significance of these vacuoles is discussed further on.

V. THE NISSL BODIES.

RHODE ('04a) has called attention to certain similarities of structure in the ganglion cells of vertebrates and invertebrates. Both have the following facts in common: (1) a homogeneous hyaloplasm, (2) a spongionoplasmic groundwork which consists of coarse and fine fibrils, (3) a *stainable substance* which in the case of the invertebrates and a part of the vertebrates is lodged in the coarse fibrillar spongionoplasm. In the remainder of the vertebrates it clumps and forms the NISSL bodies, which are, indeed, independent of the spongionoplasm, which appears between them in almost colorless fibrils.

The structures known as NISSL bodies or granules furnish a most interesting field of research. The great degree of variability in the appearance of nerve cells from different animals has led to the belief that structures existing in one nerve cell may have no counterpart in another. Among the invertebrates the failure of some authors to identify structures closely similar to those found in vertebrates has led to the supposition that such structures were lacking. It seems evident that such bodies as NISSL granules must be present in the cell for some specific purpose. The nerve cells of invertebrates have fundamentally similar functions to perform as the cells of vertebrates. If this be true, may we not expect to find some structure, perhaps even morphologically and chemically different, which takes the place of that structure known as the NISSL granule? We are of the opinion that such bodies do exist.

The *stainable structures* of the cell, referred to above, have received various names, as they have been observed and described by different authors under dissimilar conditions. The terms chromatic substance, chromophile substance, tigroid substance, sigroid substance, basophile constituent, etc., have all been employed to designate the structures recognized by us as NISSL bodies or NISSL granules. Various authors have recognized the fact that

these bodies may vary in size, in number and in capacity for taking up various staining agents.

NANSEN ('87) described the structure of the nerve cells of *Patella vulgata*, *Nereis*, *Lumbricus*, *Homarus vulgaris*, *Nephropa norwegicus* and six different Ascidians which he classed with the above. He found in the cells of the Nereidæ structures which correspond very closely in description to the granules commonly known as Nissl bodies. Some of the granules were very large and prominent and were situated in the mesial part of the protoplasm. In preparations fixed with osmic acid and stained with hæmatoxylin they were very dark, almost black in color, and consisted of a fatty (myeloid?) substance (Fig. 9).



FIG. 9.



FIG. 10.

FIG. 9. The yellow granules are scattered through the cytoplasm and are drawn with heavy outlines. After NANSEN ('87, Fig. 54).

FIG. 10. Crayfish. Shows the chromophile bodies spindle shaped and apparently associated intimately with the fibers. After PFLÜCKE ('95, Fig. 10).

Nissl bodies in invertebrates.—The question as to the existence of NISSL granules in the nerve cells of invertebrates has more than once been raised. PFLÜCKE ('95) undertook the investigation of the finer anatomy of the nerve cells of the crab, snails and worms. In the crab he succeeded in demonstrating granules which appear like the commonly accepted Nissl bodies. In the snails and worms he failed to identify such structures (Fig. 10).

MCCLURE ('97) found (chromophilous) granules in the nerve cells of *Helix* and *Arion*, and expressed the opinion that this chromophilous substance is homologous with that found in the nerve cells of vertebrates.

FLOYD ('03) was unable to differentiate by means of methylene blue any Nissl bodies in the ganglion cells of the common cockroach. In well fixed material, however, he found varying quantities of deeply staining granules and masses.

Distribution.—These deeply staining granules were found by RHODE ('04a) in both vertebrates and invertebrates to occupy a zone of the cytoplasm surrounding the nucleus but not extending out to the cell wall. A rather broad zone (the spongoplasm) at the periphery of the cell is free from these bodies, so that the ganglion cell resembles the *Amœba* in that it has a light ectoplasm and a dark entoplasm. Only the finely granular hyaloplasm enters into the axis cylinder.

McCLURE ('97) found the granules to be arranged chiefly in rows, but at certain points in the cell body they appeared to be collected into spindle-shaped groups, having their long axes parallel to the periphery of the cell (see Fig. 11). A statement of McCLURE's is of particular interest: "The cell bodies stain a deep blue, while the axis cylinder processes are only partially affected by the stain, and thus appear light in color. The cause which produces this difference is fundamentally the same in both cases: namely that the intense staining capacity of the cell body, and the lack of the same for the axis cylinder process in *Limax* are due respectively to the presence and absence of the chromophilous granules. The Flemming-iron-hæmatoxylin preparations are especially interesting for the reason that they show with great clearness, not only the same chromophilous granules but also certain spindle shaped structures in the cell body, which in all probability are collections of some small chromophilous granules. The above results concerning the presence of chromophilous granules in the nerve cells of Gasteropods point toward the acceptance of the view that this chromophilous substance is homologous with that found in the nerve cells of vertebrates (NISSL bodies)."

PFLÜCKE ('95) found that in the crab the chromophile granules of the nerve cells are arranged in rows, and in the nerve processes they were few in number. The granules were especially numerous about the nucleus, being regularly distributed. Under high magnification they were found to be spindle-shaped and to be arranged in parallel concentric rows.

FLOYD ('03) finds the granules disposed in areolar fashion in the cell, deposited upon the cyto-reticulum.

Physical constitution.—Among vertebrates the NISSL bodies have been found by FLEMMING, VON LENHOSSÉK, MARINESCO, VAN GEHUCHTEN, HELD, CAJAL, PFLÜCKE, EWING, CARRIER and others to have a granular structure—to be in reality aggregations of minute particles of deeply staining substance. FLOYD and McCLURE have presented evidence of the same structure for the NISSL bodies of the invertebrates.

Resistance to degenerative change.—The work of EWING ('98) upon cadaveric changes taking place in the ganglion cells of brains and cords of rabbits which were allowed to decompose in the air from 48 to 72 hours may give evidence as to the function of the NISSL granules. During the first twenty-four hours there was noticed a granular disintegration of the chromatic substance. This disintegration was evidently due to the separation from each other of the granules which made up the NISSL bodies. As the degenerative changes proceeded, the granular disintegration became more and more marked. During this time the individual granules retained all of their natural capacity for stains. Later when putrefaction changes were set up in the cells the NISSL granules exhibited a remarkable resistance to the action of the bacteria and still retained distinct outlines even when the cells were becoming filled with vacuoles or when the cell consisted merely of a nucleus with a narrow fringe of granules (see Figs. 12-13).

Do NISSL granules exist in the living cell? The existence of the NISSL granules in the living cell has been seriously questioned by several prominent observers and various answers have been published. DOGIEL, HELD, RUZICKA, FLEMMING hold to the view that they are an aggregation of material produced in the cell at the time of fixation, by the reagents employed. OLMER ('01) contends that the material of which the NISSL bodies are composed is scattered through the cells, and that these particles are clumped and precipitated by the fixing agent.

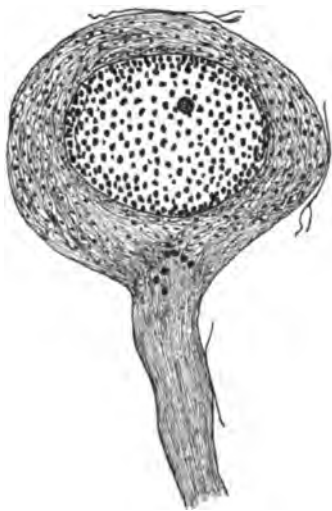


FIG. 11.

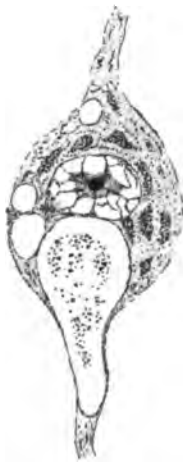


FIG. 12.



FIG. 13.

FIG. 11. *Helix*. Cell from infra-oesophageal ganglion. FLEMMING's sol., prog. iron-hæm. Concentric arrangement of fibrils and granular rows. Spindles. Pigment granules at base of process. After McCLURE ('97, Fig. 12).

FIG. 12. Medullary stichochrome of infant, 3 hours after death. LANG's fluid. Methylene blue. Very rapid and extreme vacuolation. Coarsely granular appearance of chromatic bodies. After EWING ('98, Fig. 1, plate 2).

FIG. 13. PURKINJE cell of rabbit, after 48 hours exposure to air. LANG's fluid. Methylene blue. Extreme vacuolation. Growth of putrefactive bacteria. The chromatic reticulum and bodies are reduced to a series of coarse dark granules. Complete nuclear chromatophilia. Shrinkage and destruction of dendrites. After EWING ('98, Fig. 3, plate 2).

The admirable work of CARRIER ('04) gives strong evidence for the belief that the NISSL bodies are not due to postmortem changes but actually exist in the living cells. In support of the same view may be mentioned the results by ARNOLD, VON LENHOSSÉK, CAJAL, TURNER, etc.

Our own work, done upon the living nerve cells, has convinced us beyond any possibility of doubt of the actual existence of these structures in the living cell. The detailed discussion of this feature appears later in the paper.

Studies upon the molluscan nerve cells.—In a previous paper in this *Journal* SMALLWOOD ('06) described certain morphological characters of molluscan nerve cells. Without indulging in vain repetition, it is perhaps well to call attention here to certain of these facts. There were found in the nerve cells of *Haminea solitaria*, *Venus mercenaria*, *Planorbis* and *Limax* cytoplasmic vacuoles containing a colorless, transparent liquid, also solid bodies of various sizes, irregularly rounded forms of varying numbers. The solid bodies were of different appearance in the different genera named, and somewhat different in distribution, those occurring in *Limax* being always found within the limits of the vacuoles, while in the other forms the bodies or granules were only rarely to be seen in the vacuoles. Attention was called to the fact that these bodies could be seen in the living nerve cell, and hence could not be considered as artefacts. The fact that the number of these bodies present in a given cell varies from time to time convinced us that a morphological study could not satisfactorily account for their presence and variable appearance.

In our discussion of our work upon the bodies mentioned above we do not wish to be understood as maintaining that these structures are in every sense homologous with the NISSL granules of vertebrates. Morphologically and chemically they may not correspond to the NISSL granules of vertebrates, and may even differ much among themselves in these respects. We are convinced, however, that the question of function is more fundamental and believe that these structures will be found to fill the same place in the economy of the invertebrate nerve cell as does the NISSL body of the vertebrate nerve cell.

Since the bodies found in the cells of *Limax* more nearly correspond to those found in vertebrates we will first describe our experiments upon this form and later discuss our work upon the other forms under the caption "Pigment."

Experimental.—The experimental work in connection with our study of the molluscan nerve cells has been carried out with a view to determine, if possible, the nature of some of the structures which have been found to exist in the cells. In order to insure a certain

degree of accuracy in the work it was found desirable to bring the animals into the laboratory and keep them under definite environmental conditions, which could be more easily controlled. The temperature and surroundings were generally more uniform than they would have been outside of the building. The animals were kept in moist boxes or glass dishes. Some were fed upon grass or chestnuts; others were starved. At intervals animals were taken from both the fed and starved groups and their nerve cells studied, either in sections or in the live condition.

Limax.—The remarkable appearance of the vacuoles and granulations in the nerve cells led us to make a series of tests with a number of fixing agents in order to assure ourselves that we were dealing with actual structures and not artefacts due to faulty fixation or preservation.

The following agents were employed: CARNOY's fluid, PETRUNKEVITCH's solution, picro-nitric acid, FLEMMING's strong solution, osmic acid and absolute alcohol. The vacuoles and the bodies contained within them appeared with a constancy that was remarkable.

Effects of starvation and feeding.—Specimens of *Limax* taken in the early spring as soon as they emerge from their hibernation exhibit in the cytoplasm of the nerve cells collections of vacuoles of various sizes, scattered about in various parts of the cell. Sometimes the whole cytoplasm appears to be peppered with them; sometimes they are packed together with their thin walls touching each other in such a way as closely to resemble in appearance a mass of soap bubbles. In some of the vacuoles small granules of various shape may be found. The granules are, however, not to be found in all of the vacuoles at this time. Fig. 1 of Plate I is a photograph showing the strongly vacuolated condition which may be seen in the cells and also indicates the presence of some of the granules mentioned in certain of the vacuoles.

The other cell structures do not show any especially important features. The nucleus is large and well defined. In some cases the cytoplasm appears to be somewhat shrunken, but this is far from being a constant character.

Later in the spring animals taken into the laboratory and studied, or animals which have been kept in the laboratory and fed upon grass show that the number of solid bodies within the vacuoles has increased. This increased number is found to hold throughout the summer and fall of the year.

Two possibilities for the increase in the number of bodies in the vacuoles present themselves, either the bodies are to be considered as storage products which may be called upon in time of stress to supply energy for the nerve cells or they are to be considered as degeneration products which have accumulated in the cell during the increased activity of the animal in the active season. If they are of the former class, any great increase in the activity of the animals should have the effect of breaking them down and should cause them to disappear. If they are of the second class, prolonged activity should bring about an increase in their number and size.

Fatigue.—HODGE and others have noticed that the nerve cells of animals respond to excessive stimulation in definite ways. HODGE found that the cytoplasm of the cells took on a different appearance and that the nucleus became shrunken. Our work upon *Limax* has failed to confirm these particular observations and has convinced us that we have here conditions which may have escaped notice.

An active, living, specimen of *Limax* was taken and by means of an induction current applied to the posterior part of the body forced to crawl until it could no longer draw itself away from the point of stimulation—a period varying somewhat with different specimens, but usually from one-half to three-quarters of an hour. The nerve collar was then dissected out, fixed, sectioned and stained in the usual manner. The nerve cells of an animal treated in this way differ in a very marked degree from those of the normal rested animal. In the periphery of the nerve cells are to be found the vacuoles to which attention has already been called. These vacuoles are usually numerous, but differ from those found in the normal, well fed, rested specimens in that they contain no dark solid bodies. The limits of the vacuoles are sharply marked. The vacuoles appear in various parts of the cytoplasm and may occupy nearly all the space between the nucleus and the cell wall, when at their greatest development. It is evident that these vacuoles are filled with a liquid substance, for when the cells are placed in a medium of higher concentration than the body liquids an osmotic action takes place which draws out water from the vacuoles and finally ends in their collapse.

One may say that the disappearance of the dark bodies from the vacuoles is not the result of the fatigue of the animal, but rather

the effect of the current upon the nerve cells. To avoid the possibility of this criticism another experiment was devised.

A number of well fed snails which had been living upon damp earth were taken. A part of these were killed at once and the rest were fatigued by poking them with a sharp needle until they would no longer withdraw from the point of stimulation. This process was somewhat slower than the fatigue by means of the electric needle and took from two and a half to three hours. A comparative study of the two sets of animals revealed conditions entirely in harmony with the previous experiment. The nerve cells of the rested animals show the presence of the vacuoles with the bodies in them, the nerve cells of the fatigued animals show the presence of the vacuoles but the solid bodies have disappeared. Evidently there has been some change in the cells of the animal due to the excessive amount of work which the animal was called upon to do.

Up to this time in our work no attempt had been made to ascertain whether it were possible to see these structures in the living nerve cell. It was our good fortune to find that with care in manipulation and careful observation it was possible clearly to distinguish these several structures in the living nerve cell. A trace of methylene blue added to the salt solution in which the cells were examined brought out the bodies with great distinctness within a few seconds and they could be easily studied.

The next step in our work was to study the disappearance of the bodies in the nerve cell under the microscope—to watch the process. The results were even better than we had hoped. Small electrodes of platinum foil were attached to a slide and the nerve cells mounted between these electrodes. The electrodes were connected with the secondary coil of an inductorium. Under the $\frac{1}{2}$ inch oil immersion lens the bodies in the vacuoles showed with great clearness and sharpness of outline. When the current was first applied there was no change in the appearance of the bodies but within a few minutes a change appeared. The outline of the body lost its sharpness. The body seemed to grow larger in size. The line of demarcation between the solid body and the liquid became less and less distinct and finally disappeared. The substance of the body appeared to be going into solution in the liquid of the vacuole. At the same time, there was a slight change in color, the body taking on the color of the liquid. This process

was allowed to continue until the body had been completely replaced by the more transparent liquid mass. At this time the current was stopped. A continued study of the cell showed that in the same vacuoles where the disappearance of the bodies had been noted there was later a reconstruction of the solid body. Within an hour or two the solid masses had again become established in the cells. These bodies were, however, not the same bodies as had existed in the cells previous to the stimulation, as they exhibited entirely different forms.

That we have here substances in the cell which are intimately connected with the normal activities of the cell seems to be demonstrated. As to the chemical nature of these bodies we have only little knowledge. The fact that they are more or less darkened by osmic acid would indicate that they are of a fatty nature. Further we can not say at the present time.

VI. PIGMENT.

NANSEN ('87) was, so far as we are aware, the first to give an accurate account of the yellow pigment granules existing in certain of the invertebrate nerve cells, although such granules had been observed before. He found in the nerve cells of *Patella* plenty of large yellow granules lying in the cytoplasm. These granules had a variable size, and no regular shape, being sometimes spherical, sometimes square or polyhedral. They looked as if they had been produced by the coagulation of a homogeneous yellow substance. The granules were sometimes found scattered through the whole mass of protoplasm, but more frequently were concentrated in special parts of the cells, especially in the neighborhood of the nucleus. Plenty of similar smaller and larger granules were also to be found outside the ganglion cell. They frequently occurred in such numbers that one, for a time, could feel disposed to believe that they belonged to a substance extending through the whole nervous system. NANSEN was convinced that they were either exuded from cells, or that they sprang from destroyed cells. He had observed such a substance exuded from the protoplasm of the cell. Fig. 9 represents such a case. The substance here occurred inside as well as outside the cell. The granules were concentrated toward the part of the cell surface where they were probably to be exuded. Outside the cell they were united into larger pieces of irregular shape. The granules were situated not only near the surface of the cell but also occurred in the mesial parts of the protoplasm. NANSEN recognizes that the granules gave the yellow color to the nervous system of *Patella*, as well as other molluscs. He thought the yellow color to be due to a substance allied to or similar to hæmoglobin, and also believed that the granules contained fat. He found difficulty in recognizing these granules in the sections of nerve cells. As to function, he believed them engaged in the nutrition of the cell.

McCLURE ('97) in connection with his studies of the chromophile granules mentions the existence of pigment granules in the cells of gasteropods, but gives them no further attention.

LEGENDRE ('06) found in the nerve cells of *Helix aspersa*, *Helix pomatia* and *Arion rufus* pigment granules of various sizes, sometimes isolated, sometimes grouped together in irregular masses. The granules were most frequently located in the cone of origin of the axone, though they were sometimes arranged in concentric rows in the peripheral layer of the cytoplasm. Frequently they extended out along the axis cylinder. Osmic acid alone or in combination attacked the granules and stained them black at times; at other times they were unaffected. Hæmatoxylin gave them a brown color. These reactions resembled those of the lipochrome pigments observed in the nerve cells of a large number of vertebrates and some invertebrates. The number of granules varied in different individuals, and the author had failed to establish any connection between their appearance and the physiological state of the animals. He says, "The rôle of the granules is not known. One may consider them as a food, a reserve material, a functional precipitate, a product of disassimilation, a degenerative product. The multitude of hypotheses tells us nothing concerning their composition, their variation or their functions."

Planorbis.—In the preliminary study of the nerve cells of *Planorbis* the same general methods were employed as in the case of *Limax*. A number of fixing fluids were used and their comparative effects carefully studied. The various cell structures appeared almost equally well in the cells fixed by all the different agents. From a study of a large number of sections it appeared that absolute alcohol was at least as good as any other. For clearness and sharpness of detail it could hardly be surpassed. One feature should be mentioned. A long continued stay in alcohol is not good for this material, as it tends to swell the pigmented bodies in the nerve cells and to remove from them a portion of their color, changing it from a bright golden brown to a lemon yellow. These bodies are, however, clearly distinguishable in our sections, even when the stay in the alcohol was somewhat prolonged.

The vacuoles which formed so constant a structure in the nerve cells of *Limax* are rarely found in the cells of *Planorbis*. When present they are usually located in the end of the cell farthest from the axone and very seldom contain pigmented granules, though specimens have been found in which even in the living cell it was possible to see these bodies within the limits of the vacuole. The contents of the vacuole is a liquid of low viscosity, for the little brown granules could be seen dancing with the characteristic Brownian movements. In other parts of the cell where the bodies do not appear in the vacuoles they lie perfectly at rest.

Effects of starvation and feeding.—In *Planorbis* the number and size of the pigmented granules depends upon the general

nutritive conditions under which the animal is placed. The changes in appearance, however, of the nerve cells are so slow that it has been necessary for us to extend our observations over a period of two years in order to satisfy ourselves of their correctness. Specimens have been taken from their natural habitat at various times of the year, have been kept in the laboratory under fairly constant conditions, have been fed or starved as we wished, and have finally been killed and their nerve ganglia examined.

In the summer and autumn specimens, these golden brown bodies are rounded granules of somewhat irregular shape, and varying in diameter from 1 to 5 μ . In specimens kept in the warm laboratory for a considerable time (up to three months) without feeding a distinct change is noticed in the appearance of the cells. The pigment bodies become distinctly smaller, in some cases becoming so small as not to be easily distinguished from each other even with the $\frac{1}{2}$ inch oil immersion lens. Under these conditions it is of course impossible to measure them. No bodies as large as 5 μ were found at all and only an occasional one so large as 2 μ . The substance is in the process of being broken down. It becomes very finely divided and seems to become actually less in amount in the cells. These changes take place so slowly that it is a difficult matter to follow them and only by a long series of observations can one be at all sure of any change in the condition of the pigmented matter.

In specimens taken early in the spring, which have passed the winter in hibernation, the bodies are not as a rule numerous, though some still remain in the cells. Judging from the appearance of the nerve cells of animals which had been kept in the warm laboratory during most of the winter and those which were taken early in the spring, it would seem that the processes of metabolism had been much greater in the specimens kept in the warm room and that the total amount of matter stored up was in both cases somewhat in excess of the amount which would ordinarily be needed for the use of the cells.

Fatigue.—On account of the fact that this snail, like many others, withdraws into its shell when disturbed, it was found impossible to subject it to the same conditions for producing fatigue as in the case of *Limax*. It was possible to remove the ganglia, to place them upon a slide between electrodes and to stimulate the nerve cells directly by means of induction currents. As a result

of such stimulation it was found that, unlike the granules found in Limax, these bodies are extremely resistant and would not change in appearance during the time which the cells would live under these unusual conditions. This fact, as well as their different appearance in the cell, indicates that they are of a different nature from those in Limax. They are, however, a storage product and have to do with the nourishment of the cells during times when proper food is unavailable.

Nature of the bodies.—Many experiments have been made to determine the chemical nature of the golden brown bodies, and while we cannot say definitely just what the substance is we are in a position to state to which general class of substances it belongs. It is even possible that the bodies are not of constant composition. Most of the tests used require a long time for their action, and in some cases even failed to act at all. Osmic acid blackens the bodies after a long time. In many of the specimens the blackening was merely superficial, indicating that the substance is a highly resistant or that it is not a fat but some substance which may break up into a fat and some other substance. The tests with Sudan III and with cyanin indicate the same thing. With Sudan III the bodies assume an orange color for a short time. The color soon disappears, however, and leaves the body a sort of yellow lemon color. With cyanin the action is slow. The bodies stain a deep blue, which is sometimes temporary and sometimes more lasting. In ether the bodies swell up and clump together, becoming gradually dissolved and diffused throughout the cell. The resistance of the granules is shown by the fact that it requires frequently an hour or more to dissolve a granule $1\ \mu$ in diameter.

On account of the difficulty in making these tests it was thought for a time that they might be proteid in character, but all attempts to digest them with pepsin have so far failed. The results of the tests seem to indicate that they are some sort of a fat.

Further tests with concentrated sulphuric acid indicate that the pigment is one of the lipochrome group, the bodies assuming a bright blue color as soon as the acid touches them.

Venus.—Our experiments upon the nerve cells of the edible clam, Venus, have been few in number and serve only to add emphasis to what has already been stated. We find in the nerve cells certain yellow spots, whether solid or semifluid in character we are at present uncertain. The color is not the same as that of

the bodies in *Planorbis* and they are of larger size. When tested with Sudan III and cyanin they give the colors which are characteristic for fats.

The cells of *Limnea* contain granules so closely similar to those of *Planorbis* that we have yet to find any way of distinguishing them. The pigmented granules are of the same color, size, and position in the cell. They also react in the same way to the various tests. We have not had opportunity to observe any seasonal changes in their appearance.

In the cells of *Melantho* we find a pigment of a light yellow color. The granules are generally smaller than those found in *Planorbis* and *Limnea*. This is evidently a different sort of substance, for it does not give a blue test with sulphuric acid. We have not yet made sufficient study to make a definite statement as to its chemical nature.

VII. THE CENTROSOME IN NERVE CELLS.

A few years ago the centrosome was all the fashion among biological works. The question of its origin, use and fate furnished the basis for many papers. With the accumulation of a considerable number of facts, it became evident that no general homology was to be established for the centrosome; nor did its detailed structure permit of reducing all centrosomes to a common form. About the only feature generally agreed upon was that the centrosome was at the center of radiation. In order to be sure that the dark staining granule or granules or vesicle when found in various parts of the cytoplasm has any claim to be regarded as a centrosome, it must have astral radiations. The question of the sphere substance which immediately surrounds the centrosome is more indefinite and less clearly defined than that of the centrosome. It may assume a variety of appearances and probably plays an unimportant part.

While centrosomes were being recognized in a great variety of cells, VON LENHOSSÉK ('95) was the first definitely to announce the presence of centrosomes in nerve cells. His observations were on the moderate sized spinal ganglion cells of the frog. He found the nucleus occupying in some cells an eccentric position and flattened or slightly concave on the side nearest the cell center. In this larger region of the cytoplasm there was a concentric figure in the center in which he located minute granules.

LEWIS ('96) describes in the giant ganglion cells of an annelid centrosomes on one side of the nucleus—the one toward the center and the one which tends to be

flattened or concave. The sphere varies somewhat in size, but its diameter is approximately one-third that of the cell. In some cases it is quite sharply marked off from the surrounding protoplasm of the cell; in other cases the transition to the surrounding protoplasm is so gradual that it is impossible to define its limits with precision. In the center of the sphere there is a highly refractive body, or occasionally two or three such bodies. From this central corpuscle there are in many preparations radiations which transverse the whole sphere. The rays are due to the close arrangement in radiating lines of granulations of the ordinary size. Some of the rays are very distinct, others much less clear. They are few in number, usually separated by rather uniform intervals, but often interrupted over an arc of many degrees. The central corpuscle (or corpuscles) is very distinct. It is sometimes spherical, sometimes elongated so as to look like a short rod. It shows a remarkable affinity for stains, being always colored much more deeply than any other part of the sphere.

McCLURE ('97) finds in certain cells in the ganglia of *Helix* structures which he has been pleased to designate as centrosomes. In certain unipolar cells of *Helix* which have a transverse diameter ranging between 17 and 22 μ , the nucleus was found in longitudinal sections to have an eccentric position. In addition to this, in such cells the side of the nucleus directed toward the axis cylinder pole of the cell was often flattened, or more frequently invaginated, so that the nucleus presented a kidney-shaped appearance. The flattened or invaginated side of the nucleus was never found to be directed exactly opposite to the base of the axis cylinder process, but always to a point one side of it. In the body of the cell, directly opposite the invagination, a disk-shaped structure was found. The contents of the disk was finely granular but so far as could be determined there was no evidence of radiation. At about the center of the disk two or three small granular bodies were present which stained much deeper than the surrounding granules and which are taken to be centrosomes (Mikrocentrum).

HAMAKER ('98) described in the nerve cells of *Nereis* structures to which the term centrosome was given. He found from two to as many as ten in a single cell, each one consisting of a deeply stained granule. *No radiations were seen.*

KOLSTER ('00) represents in *Cottus scorpius* deeply stained granules with no radiations, which are designated as centrosomes.

RAND ('01) states that there is commonly present in the nerve cells of *Lumbri- cidæ* a centered system consisting of centrosome and radiations. The single centrosome (or rarely two, or even three, small granules lying close together) is found in the axis of the cell, on the side of the nucleus opposite the nerve process, and therefore on the side of the greatest cytoplasmic mass. It is generally not far from the nucleus and approximately at the center of the cell as a whole. Radiations consisting of fibrils bearing minute granules extend from the centrosome toward the periphery of the cell. Calling these "primary radiations," there may also be distinguished secondary radiations, which arise from certain of the large granules in the course of the primary radiations. In rarer cases tertiary radiations may be found arising from granules in the secondary radiations. The centered system is, therefore, a complex one, consisting of a chief center or centrosome, and numerous inferior centers situated throughout the cytoplasm, all with their corresponding sets of radiations, the whole system forming a network whose complexity increases toward the periphery of the cell. In most cases no structure which could be called

a centrosome is present. The centrosome, when present, as well as each of the inferior centers, is generally surrounded by a small clear space.

The structure which LENHOSSÉK designated as a centrosome received its correct interpretation only when the toad was studied during hibernation. LEVI ('98) in describing the changes in the nerve cells during hibernation gives a minute account of the so-called concentric figure or vortex as it occurs in the toad. During hibernation the deeply staining granular substance does not appear and the other parts appear more clearly. The centrosome is nothing more than a transverse section of the axis of the vortex which is composed of fibrils. These results of LEVI throw serious doubts on the correctness of other observations which were published soon after LENHOSSÉK's. Furthermore, we do not believe in the light of all that has been recently discovered in the cytoplasm of nerve cells that the structures described by MCCLURE, HAMAKER, and KOSTER are centrosomes at all, but probably belong to one of the classes of granules. The fewness of the radiations in the results of LEWIS and RAND is of itself enough to suggest a reasonable doubt as to their actual presence, while the secondary and tertiary systems of radiations as figured and described by RAND are not in harmony with the ordinary aster structure. That the centrosome is not usually found in adult nerve cells is abundantly shown by numerous investigations; that it does appear in some nerve cells cannot be doubted, as HATAI ('01) has shown in the young rat. The centrosome is more easily seen in the young nerve cell than in the adult, which he believes indicates a slight tendency to the degeneration of this structure. Most of the results referred to above are so questionable that we are inclined to believe that there is very little positive evidence in favor of the centrosome in adult nerve cells.

SUMMARY.

1. The nervous system of gasteropods does not permit of direct stimulation of a specific ganglion because of the compactness of the nerve collar and the numerous nerves arising from the different ganglia.

2. Lymph canals are not identical with the cytoplasmic vacuoles. They really exist, and have a rather general distribution among the nerve cells of invertebrates.

3. Vacuoles are present in the cytoplasm of nerve cells of Nemerteans, Annelida, Crustacea, Insecta, and Mollusca. The vacuoles can easily be seen in the living cells as independent structures filled with a fluid or differential bodies. They are transitory structures, vary in number and are not limited by distinct walls.

4. NISSL bodies exist in invertebrate as well as vertebrate nerve cells. They are found to occupy a zone of cytoplasm next to the nucleus but not extending out to the cell wall in most instances. They are chiefly arranged in rows or in spindle-shaped groups.

The NISSL bodies are aggregates of extremely minute particles and exhibit marked resistance to degenerative changes. They actually exist in the living nerve cell. Those occurring in *Limax* are always found within the limits of the cytoplasmic vacuoles. They can be caused to appear in the cell by rest and feeding and can be made to disappear through hibernation, fatigue and electrical stimulation. They are probably of a fatty nature.

5. Pigment granules are found very generally in molluscan nerve cells. They do not readily respond to starvation experiments, can be increased in size and number through feeding, are practically unchanged by fatigue or electrical stimulation, but do show occasional variations in size and number. These bodies respond to the tests indicated for lipochrome substances or fats.

6. The centrosome has been described in many of the invertebrate nerve cells, but there is considerable doubt as to its persistent presence in adult nerve cells.

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84 *Journal of Comparative Neurology and Psychology.*

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PLATE I.

FIG. 1. Photograph of a section of ganglion of *Limax*, fixed in absolute alcohol and stained by iron-haematoxylin. The cells show many vacuoles of various sizes in the cytoplasm, some of which contain solid bodies.

FIG. 2. Same as above, under higher magnification, $\frac{1}{2}$ inch oil immersion lens used in making photograph.

FIG. 3. Photograph of a living nerve cell of *Planorbis* under $\frac{1}{2}$ inch oil immersion lens. Note the very large nucleus and mass of pigment granules at the axone hillock of cell.

FIGS. 4 AND 5. Photographs of sections of ganglion of *Planorbis*, fixed in osmic acid, unstained. The dark bodies are the same as those shown in Fig. 3.

DOCUMENT I OF THE REPORT OF THE PRESIDENT OF THE BRAIN COMMISSION (Br. C.).

In the spring of 1906, the Imperial Academy of Sciences at Vienna issued to the Associated Academies a report on the condition of the interacademic institutes for brain study. This report appeared in two documents (A) and (B), the former of which (A) contained the earlier correspondence relating to the institutes for brain study, the names of those at that time members of the Central Commission for brain study, and the provisional order of business and program proposed for the meeting of the Brain Commission (Br. C.) to be held in Vienna at the end of May, 1906.

Document (B) gave a brief historical review of the progress thus far made in the establishment of Interacademic Institutes for brain study.

I now add a report on the further course of affairs and especially on the first session of the Brain Commission, together with a report of the meeting of the Committee of the Associated Academies.

The meeting, called conjointly by the undersigned and the President of the Vienna Academy, took place on the twenty-seventh and twenty-eighth days of May at Vienna. All the members of the Brain Commission were invited. There were present besides the undersigned, the Messrs. DONALDSON (Wistar Institute, Philadelphia), EHLERS (Göttingen), FLECHSIG (Leipzig), LANGLEY (Cambridge, England), v. MONAKOW (Zürich), HERMANN MUNK (Berlin), OBERSTEINER (Vienna), and G. RETZIUS (Stockholm), GOLGI (Pavia), Dr. GREENMAN, Director of the Wistar Institute, was present at the deliberations. Detailed minutes of the proceedings were taken by Dr. MARBURG, of Vienna. These are in the possession of the President of the Central Commission for brain study. (The President at that time, and until 1909 inclusive, being Dr. WALDEYER, Berlin, N. W. 6, 56 Luisenstrasse, Anatomisches Institut). These minutes are, however, open to inspection by the several academies, as well as by the institutes for brain study and the members of the Commission.

At these sessions there was drafted a constitution, together with an order of business, and later this was revised for publication by the undersigned, with the approval of the Executive Committee. This appears as Document II of the present report, and in its revised form must be presented for final acceptance and ratification at the next meeting of the Brain Commission (Br. C.), which will occur in the spring of 1909, previous to the next session of the Committee of the Associated Academies. Moreover, the paragraphs in this document which regulate the relations of the Brain Commission to the Association of Academies, must also be ratified at the regular meeting of the Association of Academies at Vienna in the spring of 1907. In the meantime, the undersigned President, with the coöperation of the Executive Committee, will conduct the business in accordance with the provisional constitution, as given in Document II.

The accompanying Document III contains information concerning the relation of the Brain Commission to the Association of Academies.

By vote of the members, the Central Commission was enlarged. It consists at present of the following members:

Egypt.....	ELLIOT SMITH.....	Cairo.
Belgium.....	VAN GEUCHTEN.....	Louvain.
Denmark.....	F. C. C. HANSEN.....	Copenhagen.
Germany.....	1. EDINGER.....	Frankfurt a/M.
	2. EHLERS.....	Göttingen.
	3. FLECHSIG.....	Leipzig.
	4. H. MUNK.....	Berlin.
	5. WALDEYER.....	Berlin.
England.....	1. LANGLEY.....	Cambridge.
	2. SHERRINGTON.....	Liverpool.
	3. V. HORSLEY.....	London.
France.....	1. DEJERINE.....	Paris.
	2. RAYMOND.....	Paris.
Japan.....	SHUZO KURE.....	Tokio.
Italy.....	1. GOLGI.....	Pavia.
	2. LUCIANI.....	Rome.
	3. ROMITI.....	Pisa.
Holland.....	WINKLER.....	Amsterdam.
Norway.....	GULDBERG.....	Christiania.
Austria-Hungary.....	1. S. EXNER.....	Vienna.
	2. OBERSTEINER.....	Vienna.
	3. V. LENHOSSEK.....	Budapest.
Russia.....	1. BECHTEREW.....	St. Petersburg.
Sweden.....	2. A. DOGIEL.....	St. Petersburg.
	1. HENSCHEN.....	Stockholm.
	2. G. RETZIUS.....	Stockholm.
Switzerland.....	V. MONAKOW.....	Zürich.
Spain.....	S. RAMÓN Y CAJAL.....	Madrid.
U. S. of North America ..	1. F. P. MALL.....	Baltimore, Md.
	2. C. S. MINOT.....	Boston, Mass.
	3. H. H. DONALDSON.....	Philadelphia, Pa.

Thirty-one members in all.

At the suggestion of the members assembled in Vienna, the undersigned will put himself in communication with Australia, with the purpose of selecting a member of the Commission to be elected from that country. (A letter has been sent to Dr. WILSON in Sydney).

The large number of members, and their selection from different countries and nations will serve only to advance the cause. Besides this a large membership is necessary in order that at the triennial meeting of the Brain Commission, the desired number of members may be present. It may be remarked that only 8 of the 18 members were able to be present at the last meeting. The same conditions may be looked for in the future. Suggestions as to further elections, particularly from countries not yet represented, will be gladly received. These may be forwarded to the present President.

The proposals, especially those concerning the Executive Committee, made by the President in the previously mentioned Document (A), were accepted.

The Executive Committee is composed for the present of the following gentlemen:

1. W. WALDEYER, Berlin, President of the Br. C.
 2. H. OBERSTEINER, Vienna, Vice-President.
 3. E. EHLERS,
 4. P. FLECHSIG,
 5. H. MUNK,
- } Members.

The reason why the members of the Executive Committee have been chosen thus far solely from Germany and Austria, is merely to facilitate communication with the present President whose home is in Berlin, but this arrangement must not be regarded as establishing a precedent.

Owing to vacancies caused by death, certain changes became necessary in the special commissions established in London in 1904 for the several departments of brain research. These changes were made at the meeting in Vienna in May, 1906, and are as follows:

RETZIUS was made President of the Commission on Embryology, and DONALDSON was named on this commission in the place of SCHAPER, deceased. On the Commission on the Pathology of the Brain, MINGAZZINI was named in place of WEIGERT, deceased.

At present the seven special commissions are constituted as follows:

I. Commission on descriptive Anatomy. WALDEYER (President), CUNNINGHAM, MALL, MANOUVRIER, ZUCKERKANDL.

II. Commission on comparative Anatomy. EHLERS (President), EDINGER, GIARD, GULDBERG, ELLIOT SMITH.

III. Commission on histological Anatomy. GOLGI (President), RAMÓN Y CAJAL, DOGIEL, VAN GEUCHTEN, LUGARO.

IV. Commission on Embryology. RETZIUS (President), BECHTEREW, DONALDSON, v. LENHOSSÉK, C. S. MINOT.

V. Commission on Physiology. H. MUNK (President), V. HORSLEY, LUCIANI, MOSO, SHERRINGTON.

VI. Commission on pathological Anatomy and Physiology. OBERSTEINER (President), DEJERINE, v. MONAKOW, LANGLEY, MINGAZZINI.

VII. Commission on clinical Neurology. FLECHSIG (President), HENSCHEN, FERRIER, LANNALONGUE, RAYMOND.

The following were recognized as interacademic Institutes for brain study.

1. The Neurological Institute of the Madrid University conducted by RAMÓN Y CAJAL.

2. The Neurological Institute of the Leipzig University conducted by P. FLECHSIG.

3. The Neurological Institute of the Vienna University, conducted by H. OBERSTEINER.

4. The Neurological Institute of the Zürich University, conducted by v. MONAKOW.

5. The neurological department of the The Wistar Institute, Phila., U. S. A., conducted by H. H. DONALDSON; M. J. GREENMAN, Director of the Institute.

6. The Neurological Institute in Frankfort a/ M., conducted by EDINGER.

In addition to the Institutes already recognized, The Wistar Institute in its neurological department was accepted as a Central Institute for brain study, and consequently will be regarded by the Brain Commission as the Central Institute for brain study in the United States of North America.

The Messrs. v. MONAKOW and OBERSTEINER proposed that the Central Commission should request the proper authorities in the countries mentioned below, to recognize the Neurological Institute at Zürich, as the Central Institute for Switzerland, and the Neurological Institute at Vienna, as the Central Institute for Austria. This request will be made at an early date.

In addition, reports were made on the Neurobiological Institute of the Berlin University, under the direction of O. VOGT, and on the condition of affairs in Norway, Sweden, Holland, England, Italy and Hungary.

In Sweden, Professor LENMÄLM is ready to undertake work of this sort.

In Norway, Professor GULDBERG is prepared to utilize his Institute for the same purpose.

In Holland, Professor WINKLER has taken steps to organize there an Institute for brain study. Assent has also come from Italy and Hungary. The Imperial Academy at St. Petersburg has also reported to the undersigned that the proposition for the establishment of an Institute for brain study will be favorably considered there. Finally, Messrs. BECHTEREW and A. DOGIEL in St. Petersburg, and Messrs. DARKSCHEWITSCH in Kasan, and ROTH in Moscow, have announced their willingness to place their laboratories or clinics at the service of this cause.

The question whether or not a Central Imperial Institute should be organized in Germany, was considered at the session of the Associated Academies in Göttingen in October, 1906. For various reasons such a Central Institute for the united German Empire was rejected by the authorities, who much preferred to leave the organization of the Institutes for brain study to the individual states. This, however, does not prevent the larger states from establishing Central Institutes as well as local Institutes. As previously stated, the Institutes under the direction of FLECHSIG and of EDINGER, have been already recognized as Interacademic Institutes for brain study.

The Institute in Berlin, directed by O. VOGT, has not yet become connected with the Brain Commission.

As regards the recognition as Interacademic Institutes for brain study, see section xvii of the constitution. In regard to the Central Institutes and their recognition and arrangement, see section xxi.

It is not to be expected that immediately upon their inception the proposed organizations shall at once exhibit a complete activity, but by degrees, a closer union of the separate Institutes will develop, and through experience, that form of organization will be found which will make possible effective coöperation.

In accordance with Professor LANGLEY's proposal, made at the meeting of the Central Commission, one of the first steps taken will be towards the further revision of the nomenclature, with the purpose of obtaining international uniformity.

Moreover, we beg the Academies still to lend their powerful support to this undertaking which has developed through their initiative, for without such support we shall find it hardly possible to induce the several governments, in view of the many demands made upon them, to grant with the desired promptness, the means necessary for the establishment of specially planned and suitably arranged Institutes for brain study.

Finally, we beg the above mentioned Institutes, in accordance with the constitution, to furnish the Central Commission with the necessary reports as to their condition and activities, and at the same time, to assist one another through an interchange of material and publications.

By this means, in the course of time, the Institutes may hope to attain the desired completeness in the matter of collections and reference libraries.

(Signed)

WALDEYER,
President of the Brain Commission.

NEUROLOGY AT THE PHYSIOLOGICAL CONGRESS, HEIDELBERG,
1907, AND AT THE CONGRESS FOR PSYCHIATRY, NEUROLOGY,
PSYCHOLOGY AND THE NURSING OF THE INSANE, AMSTER-
DAM, SEPTEMBER, 1907.

At both of the congresses named above considerable attention was paid to topics that are of special neurological interest. Owing to the difference in the membership, the character of the papers differed in the two congresses, the papers at the Physiological Congress being largely of a purely scientific character, while those at the Amsterdam Congress treated more especially matters in connection with human diseases. In the later congress more attention was devoted to the anatomy of the nervous system than in Heidelberg, although at both the functional study was very prominent. At Heidelberg about half of the sessions of one section were occupied with papers concerned with the central nervous system and the special senses, and at Amsterdam half of the time of the section of neurology and psychiatry and some of the time of the section of psychology and psychophysics were so devoted. Many of the most prominent physiological neurologists were present at the Physiological Congress and few attended the Congress at Amsterdam, although the representation of the clinical neurologists at Amsterdam was large and most important. In addition to those whose papers are abstracted below may be mentioned: BETHE, EDINGER, EXNER, GOTCH, HERING, LUCIANI, MUNK, NAGEL, NISSE, RICHTER, SCHÄFER, v. TSCHERMAK, v. UEXKÜLL, and VERWORN at the Physiological Congress; and v. BECHTEREW, CAJAL, v. GEHUCHTEN, v. JELGERSMA, LANGELAAN, MOTT, OBERSTEINER, OPPENHEIM, WINKLER, and WESTPHAL at the Congress of Neurology and Psychiatry.

Among so many papers it is almost impossible to select those that are of most importance to the readers of the *Journal*, but the following abstracts give a fair idea of the diversity of subjects and of the character of the work presented at the two meetings.¹

Professor GASKELL (Cambridge), *A*, gave a general account of his views on the evolution of the vertebrate nervous system, which are already known to some of the readers of the *Journal*. He considers the vertebrate central nervous system to be developed phylogenetically from the coelenterate type of oral nervous ring. Ontogenetically there are two types of tissues in the body, the master tissues, connected with nervous system, and the free cells of the body which arose as modifications of the germ cells. The central nervous system has been developed from the combination of the nervous and the alimentary systems; the infundibulum is the relic of the development from the early oesophagus, the crura represent oesophageal commissures, the spinal cord is the ventral chain of ganglia, and so on. All the principal parts of the vertebrate type of nervous system were compared with parts

¹ In the report of each paper will be found after the name of the man presenting the paper a letter indicating the congress at which the communication was read: *A*, for Amsterdam; *H*, for Heidelberg.

of the nervous system in the arthropod types. The reason why ontogeny has not so far revealed this form of evolution is said to be because all the energies of the embryologists have been bent to the study of the matter from the standpoint of the germ layer theory. A new embryology is, therefore, necessary, according to GASKELL. Numerous charts and diagrams illustrated the paper, but in so limited time it was not possible to go into the matter in sufficient detail that the reader could point out the relation of the hypothesis to conditions of disease, but the main points were well shown.

"The salts of nerve, their importance to its function" was discussed by Prof. J. S. MACDONALD (Sheffield), *H.* The paper gave an account of experiments to determine the changes in the chemical composition of nerves, especially when injured. MACDONALD found that when a nerve is injured there results a precipitation of some of the colloid substance of the intramyelin material, the precipitation being accompanied by the appearance of potassium salts capable of reacting with cobalt nitrate, and of chlorides capable of reacting with silver nitrate. This change in composition is taken to indicate the explanation of the current of "injury" which is found in injured tissues, and the inference was drawn that the nerve current is about the same sort of change in the composition of the nerve, though in the normal uninjured nerve the salts do not leave the nerve, but change their position. The potassium salts are normally deposited about the nodes of RANVIER, which act as cathodes by which the electrical current leaves the fiber. There is also a deposition of the chloride salts at these points.

Further experiments to indicate the chemical character of the nerve-muscle activity were reported by LANGLEY (Cambridge), *H.* He gave the results of work to indicate that the effect produced by a motor nerve depends upon the nature of some receptive substance or substances formed by the cell in the region of the nerve ending. In such a muscle as the sartorius of the frog it can be seen that after the application of a dilute solution of nicotine the muscle contracts, but that the greatest thickening is in the regions where nerve endings are most numerous. When the nicotine is applied to points the response is found only from the parts where the nerve endings are. Other experiments with nicotine, curari, sodium chloride, and adrenalin show that there are in the muscle probably two substances, radicles, one causing the slow the other the brief quick contraction. These substances are believed by LANGLEY to be radicles of the contracting molecule in the neighborhood of the nerve ending. The functions that have been attributed to the nerve endings are in reality, according to the author, functions of the muscle plasm, and the "motor nerve endings are not organs with specific properties." It is difficult to understand the last statement in a literal manner, for the motor nerve endings must have some relation to the production of the contraction of the muscle, if it be only, and the writer believes this to be Professor LANGLEY's opinion also, that of starting the chemical change in the muscle protoplasm which we call "contraction." Curari, according to the work already finished, may no longer be considered to act on the nerve endings, but is active on the "receptive radicles" of the muscle substance, and is partly antagonistic to the action of nicotine.

Dr. R. HÖBER (Zürich), *H.*, read a paper "Der Erregungsvorgang als Kolloidprozess" in which he brought forth strongly the chemical view of nerve and muscle activity. The alterations in the excitability which are produced in muscles and nerves by the application of various salts were formerly attributed by HÖBER to the

effect of the salts on the colloid protoplasm. Later experiments of the effects of salts on albumen and lecithin have shown that there is a close relation between the effects on colloid and on the excitability. The excitability alterations produced by salts resemble corresponding (i. e., reversible) electromotor phenomena, and a connection can be shown between the alterations of excitability and the condition of the colloid protoplasm. The conclusion that the reader further drew from the results of his experiments is that normal production of excitation by the usual electrical means is accompanied by alterations in the condition (composition) of the colloid. This it will be noted is the same conclusion that was reached by MACDONALD in the paper mentioned above. This view of the nature of excitation is corroborated by the fact that the current of rest produced by the action of salts is, like the action current, retarded by various narcotics. According to the view of excitation and the action of various narcotics the nature of narcosis must be or must depend upon some sort of retardation of the colloid process normally accompanying excitation.

Dr. N. A. BARBIERI (Paris), *H*, denied that there is any regeneration in nerve fibers, after they have been sectioned. His paper contained statements not in accord with the experience of the return of function in man and other animals, and it was difficult to get the author's point of view. The abstract of his paper, "Cycle d'évolution des nerfs sectionnés" gives the following conclusions: There exists no autoregeneration of nerves. In strictly physiological evolution the peripheral end of a sectioned nerve remains inexcitable and always degenerates; the central end does not regenerate, but remains excitable and its structure remains normal. If suppuration exists the central end of the nerve also undergoes retrograde degeneration. If there be no regeneration of a divided nerve it is difficult, or perhaps impossible, to explain how the animal recovers the motor and sensory functions after an interval of time. The experimental evidence adduced by BARBIERI in support of his conclusions is not of the best, I believe, for he waited only three months for the regeneration of the vagus nerve. Had he extended his experiments over a longer period of time he would doubtless have been compelled to conclude that regeneration is the rule in respect to the peripheral nerves.

Certain nerves and parts of nerves have been long known to have an inhibitory function. Examples of this are the vagus and the so-called vasodilator nerves. The inhibitory function for the muscular nerves was shown by Professor NICOLAIDES (Athens), *H*, by demonstrations on the frog. The nerve fibers supplying the gastrocnemius muscle of the frog are from two bundles of the lumbar plexus. When the upper one of the bundles was stimulated with a tetanizing current the gastrocnemius contracted, but if immediately after the application of the current to the upper bundle the lower bundle was stimulated with feeble currents the contraction gave way to a relaxation. When strong currents were used for the stimulation of the lower bundle at the time the upper was being stimulated, the relaxation did not take place, but the original rise was accentuated. These findings can be explained only on the supposition that there are in the muscular nerves of the vertebrates inhibitory as well as excitor fibers. This conclusion, as has been hinted at above, is in accord with results from other parts of the nervous system.

Against the views of BETHE, Professor F. B. HOFMANN (Innsbruck), *H*, considered some evidence regarding the nerve endings in his paper, "Zur Frage der peripheren Nervenetze." The histological studies of the nerves going to the

heart and the smooth muscles of the vertebrates as well as to the muscles in molluscs show that in these muscle systems the nerves end not in free fibrils but in end nets. Each nerve can form a closed net for itself or there may be a continuous net formed by an anastomosis between the various nerve filaments. These nets are limited to the final branches of the nerves and are, according to HOFMANN, entirely independent of the presence of ganglion cells. The appearance of the nerve nets with nuclei is an artifact. Physiologically the innervation of the smooth muscles in vertebrates and molluscs, in so far as there are no ganglion cells present, is a localized one, and there is no general radiation of the excitation aroused in the central nervous system. Certain conclusions that would follow from this view of the matter were referred to by the speaker, and the paper was discussed by BETHE and LANGLEY.

In spinal animals, Professor SHERRINGTON (Liverpool), *H*, demonstrated the effect of "removal of stimulus from the stepping reflex of the spinal dog" and the "influence of strychnine on the reflex inhibition of skeletal muscles." A cat was shown in which all the nerves of the four feet were severed, but the animal was able to walk well and accurately. In this animal burning the feet did not produce a reflex withdrawal and there could have been no nerve conduction to the spinal cord. This suggested that an important source of stimuli for the reflexes of walking or stepping is in the proximal part of the limbs. To confirm this supposition SHERRINGTON divided the spinal cord in a dog at the tenth thoracic vertebra (the animal shown at the congress had the operation performed almost three years ago), and when the limbs of the dog were held from the ground they executed the stepping reflex. When one thigh was gently lifted the reflex immediately ceased in both legs. On allowing the thigh to hang again the reflex began immediately with the same activity as before. The reflex stepping was inhibited by pinching the tail, but on releasing the tail it began with increased activity, quicker and with greater amplitude. The antagonistic action of strychnine on the reflex inhibition of skeletal muscles was shown by SHERRINGTON in the following manner: In a decerebrized or spinal cat the vasto-crureus muscle was prepared for examination. All the other muscles of the leg were paralyzed by severing their nerves or their attachments. After this was done it was found that stimulation of the internal saphenous nerve below the knee always caused reflex relaxation of the vasto-crureus, which in normal action produces an extension of the leg. After the inhibition was obtained strychnine was injected and then stimulation of the internal saphenous nerve was followed by reflex contraction of the vasto-crureus. In some way the strychnine acted on the spinal cells to change the central inhibition into excitation.

Dr. M. PHILLIPSON (Brussels), *H*, demonstrated the movements of a spinal dog and considered the subject, "Sur les réflexes croisés chez le chien." The dog had been shown to the congress in 1904 after a complete section of the spinal cord in the dorsal region, and at that time it showed the following: Numerous direct and crossed reflexes, principally of direct extension, direct flexion, and crossed extension; when the animal was suspended vertically the feet of the animal were moved rhythmically; when hung horizontally the feet moved faster and the movements were seen to be those of walking, trotting, and galloping; when placed on the ground the feet moved to bring about the propulsion of the animal, and the feet movements were correct in point of view of coördination but strongly ataxic. In the same animal the dorsal columns of the cord in the lumbar region were extirpated to deter-

mine the part played by each of the types of reflexes, the direct and the crossed. After the second operation when the dog was suspended vertically rhythmic movements were not produced, nor were they when the animal was suspended horizontally. The left leg was moved when it was stimulated, the right not. The right leg did not contribute to locomotion. It can be said, therefore, that the direct and the crossed reflexes may be preserved independently; that the direct reflex is necessary for the foot to be kept in a normal position, but that for the rhythmic movements, especially those of locomotion, the crossed reflexes are indispensable.

A general study of the ontogenetic course of some human reflexes was reported by BYCHOWSKI (Warsaw), *A*, and from this some phylogenetic conclusions were drawn. The reflexes studied in detail were the knee kick, the tendo Achillis, and the abdominal in new-born children and during the first few months of life. He found that the knee kick was constantly present from birth, and that this reflex is more lively than in adults, which is to be explained by the lack of cerebral control. In the first month the Achillis reflex is seldom obtained. From the middle of the first year until the second year it comes more often until it is a constant occurrence. Similarly with the abdominal reflex, although it is not so constant as the Achillis reflex. These facts are taken to indicate that the Achillis and the abdominal reflexes are later phylogenetically than the knee kick; that the knee kick is purely spinal in origin; that the Achillis reflex is controlled by the midbrain, and that the abdominal reflex is under the control of the cerebrum.

Dr. NOVOA SANTOS (Santiago, Spain), *A*, reported results and conclusions of a study to determine reflex and conscious time. The time taken up by the purely mental part of a reaction has been calculated by the author from a formula that he has manufactured for the purpose, and he concludes that the mental time varies for the different senses, as follows: touch .01 second; vision, .027 second; hearing, .013 second, and so on. From the abstract and the paper it is impossible to properly criticise the work, but it is most interesting that we should find a thoroughgoing interaction hypothesis at the basis of the work.

A paper of some anatomical interest is that of Dr. S. J. DE LANGE (Amsterdam), *A*, "Sur l'anatomie du faisceau longitudinal postérieur." The author gave the results of his studies on this bundle, made on rabbits, cats, and guinea pigs. Lesions were made in different parts of the medulla oblongata, in the posterior longitudinal bundle, in the nuclei of DEITERS and DARKEWITSCH. Most of the material was examined twenty days after the operation by the MARCHI method, and a few specimens after three or four days by the NISSL method for nerve cells. In addition to personal material the author had access to material showing the effects of lesions of the cochlear nerve, the vestibular, and the trigeminal, and embryological series of the cat and rabbit. The results of the examination of this material are that the principal fibers of the posterior longitudinal bundle are descending fibers, having their origin in the nucleus of DARKEWITSCH. There are some ascending fibers at the most distal portion of the bundle, with cell bodies in the medulla oblongata, which go to the nuclei of cranial nerves. Some fibers of the vestibular nerve go by way of the bundle to motor nuclei, but there are more crossed fibers than homolateral ones. There are also some fibers from the cochlear nerve, but none of the trigeminal fibers go by way of the posterior longitudinal bundle.

Professor WINKLER (Amsterdam), *A*, reported on "Labyrinthonus." Immediately after the extirpation of the labyrinth on one side or after section of the eighth

nerve in rabbits there is found: the eye on the same side is turned down and inward as though the internal and inferior rectus functioned with the other muscles weakened. The contralateral eye is fixed outward and upward as if the abducens muscle were paralyzed. There is a fixation of the head toward the operated side and at times the neck is so much turned that the cheek or the head touches the floor. There is a decided atony of the extremities. After a time all the phenomena decrease in severity even after complete destruction of the labyrinth. Incomplete extirpation of the labyrinth as well as the extirpation of the cochlea produce the main symptoms noted above, but less completely. Bilateral extirpation of the labyrinths or the eighth nerves produces a strong atony in nearly all muscles; protrusion of the eyes which are level, but with nystagmus; the head is erect but wobbles and is often thrown back in paroxysms; the ears hang down; the back is sunk in; the legs can no longer bear the weight of the body; the animal crawls rather than walks, with the legs apart and the extremities extended. There is, therefore, a normal tonus control by the labyrinth. The removal of the influence produces inexactitude in movement, not paralysis.

An interesting report of work on the anatomical relations of the cerebellum was that of Dr. L. J. J. MUSKENS (Amsterdam), *A*, on cerebellar connections. Animals that had part of the cerebellum injured or destroyed were examined by the MARCHI method and the results were given in the paper. In the rabbit the flocculus cerebelli (lobulus petrosus cerebelli) contains cortical matter, but also a part of the dentate nucleus; after this whole lobe had been removed no degeneration was found in the restiform body or in the spinal cord, but there was a coarse degeneration of the middle third of the superior crus cerebelli. This peduncle, therefore, is not connected with the spinal cord, but is made up of strands of fibers similar to the fibers in the internal capsule. The ventrothalamic bundle of PROBST was also found degenerated in all cases. In the squirrel the flocculus contains only cortical matter and fibers, but no part of the dentate nucleus. In this animal after destruction of the flocculus the degeneration stops in the dentate nucleus. In the cat the superior crus cerebelli was found to be the seat of degenerations, but there were none in the inferior crus or in the cord. In cats, after section of the superior peduncle in front of its decussation caudal to the red nucleus, no degeneration was found in the reticular nucleus and the predorsal region, but in one animal after lesion of the tegmentum (the instrument passing through the middle peduncle) there was some degeneration of transverse fibers, which ran through the substantia reticularis, sweeping dorsally across the raphé and ascending to the red nucleus on the other side. Dr. MUSKENS concluded that the majority of the fibers of the ventral cerebello-thalamic bundle may be considered as a part of the decussation of the superior crus; the only difference is that they cross the raphé far more distally in the pons, and in the rabbit at least a number of the fibers appear to run in the crus cerebelli ad pontem.

On the physiology of the cerebellum, VAN RYNBERK (Rome), *H*, reported some experiments. This was a continuation of the work upon which he had formerly been engaged, but instead of dogs the author used sheep. The cerebellum of the sheep, it will be remembered, differs from that of the dog in that the posterior median lobule of the dog is inconsiderable, and the ansiform lobule is large, while in the sheep there is a large posterior lobule and a small ansiform lobule. Localized results followed different lesions of these parts of the cerebellum, especially those

concerned with movements of progression. When the ansiform lobule was extirpated on one side there was no observable effect. When this sort of lesion was combined with the destruction of the posterior median lobule there was ambulatory dysmetria in the homolateral forefoot (*Häbnetritt* of LUCIANI). After simple extirpation of the posterior median lobule there was always an inability to move, which was transient but for a time complete. After extirpation of the paramedian lobule there was a turning of the animal about the long axis.

Dr. W. A. JOLLY (Edinburgh), *H*, read an account of "the effects of lesions of the ascending parietal convolution in monkeys." He told of experiments that he had performed in which lesions of the ascending parietal convolution were made by the cautery, which were followed by distinct degenerations in the posterior limb of the internal capsule. When the lesion embraced all of the convolution the animals exhibited a preference for the use of the limb on the homolateral side, indicating in general that there was not so good control of the limb innervated or supplied by the nerves going to the ascending parietal (nerves for muscle sensation, probably). There was, however, no definite ataxia noted, but this is not surprising in view of the experiments of SHERRINGTON that are recorded above and other experiments by the same investigator. It is interesting that the ability to salute at the word of command remained unimpaired after the whole ascending parietal region on the opposite side had been destroyed, but the reader gave no indication of how long before the operation the habit had been formed.

The paper of LEWENDOWSKI (Berlin), *A*, was one of the most interesting at either congress, if he has excluded all other explanations for the condition he reported. The title of his paper is "Abspaltung des Farbensinnes durch Herderkrankung des Gehirns." In this he gave an account of a patient who had hemiplegia and hemianopia, but in the field of vision still remaining colored stimuli evidently did not mean color, for he could not name a color that was shown to him, or state the color of an object that was given, or select a color when the name was spoken, or match colors. According to other tests there was no definite color blindness, but there was no connection between the colors and the names of colors.

On account of the recent disputes regarding aphasia, which have been due to the investigations and writings of MARIE, the discussion of the subject by Professor VON MONAKOW (Zürich), A. PICK (Prague), LIEPMANN (Berlin) and HARTMANN (Graz) was most welcome (*A*). PICK in discussing "Asymbolie und Apraxie," dealt in a very general way with the problems, but referred especially to the meanings of the terms used to designate the different forms of disturbance in the appreciation of sensations dealing with social intercourse, that is, in the naming, understanding and in general the appreciation of the things used by all for the conveyance of ideas. He noted the three ways, all different, in which the term asymboly has been used, and urged that the term should be employed in its original sense and should be used to imply what FINKELBERG had first used it to mean, disturbances of the means of expression. If it be used in this sense it would include many of the forms of so-called aphasia, but not all. Agnosia, in WERNICKE's sense, and apraxia would not be included but considered separate subjects. VON MONAKOW entitled his communication "Aphasie und Apraxie." Aphasia, apraxia and asymboly, he said, are names for groups of conditions accompanying disturbances in a motor or sensory sphere. The conditions are large and can only be roughly outlined but they fall into two main groups: (1) in which especially the use and understanding

of the signs of language have been lost, and (2) in which orientation in space and time, recognition (by each sense for itself), is included, i. e., *sensory asymboly* and *agnosia*; or in which there is lost the ability to realize coordinated movements directed to an end, i. e., *motor asymboly* and *apraxia*. Both these groups VON MONAKOW would join under the general term *asemia*. He showed diagrams of fifty-two published cases of different forms of aphasia, with lesions in but not limited to BROCA's convolution, of which eight were permanent without improvement, two were permanent with little improvement, thirteen temporary with complete recovery, ten acute, and five with pure subcortical aphasia, while fourteen cases were negative as regards speech defects. His summary of the results is that aphasia, apraxia and asymboly are usually produced by lesions, more or less indefinitely localized, in the left hemisphere, but that sometimes, though seldom, the lesions are sharply defined. Some of these left residual conditions, while others showed the phenomena only temporarily and the disorder disappeared after a greater or less length of time. The latter type of cases fall into two groups: (1) in which the localized symptoms disappear nearly simultaneously with the general phenomena, and (2) in which the symptoms disappear after some weeks or months, perhaps years, although the form of the lesion remains unaltered. The disappearance may be gradual or all the symptoms may disappear at the same time. Some remain as permanent defects. This view of the conditions in aphasia is of special interest as compared with the views of MARIE who, to give the situation in brief, believes that all aphasic disorders are of the nature of mental defects, more or less permanent, and who does not believe that the aphasias are caused by well defined lesions in the cerebrum. VON MONAKOW believes that the sharply defined clinical forms of aphasia and apraxia are due less to the injury as such, i. e., disturbance of any number or quality of neurones, than to what he calls *diachesis*, and that the better the differentiation of the symptoms the more does the principle of diachesis come in. Diachesis, it should be noted, is the term used by VON MONAKOW to indicate the lack of stimulation of certain centers by impulses from other centers, which normally act by their impulses as stimuli to the others. In other words, it is the condition of inability of a secondary center to function because of the destruction or paralysis of the primary center connected with the given secondary center. This is placing the blame one step further back than has usually been done. Dr. HARTMANN took up the subject of what problems are to be solved for a proper understanding of the various speech defects. In regard to aphasia it may be taken as settled that the pathological conditions of asymboly and apraxia appear when both sides of the cerebrum are diseased or when one side is affected with complications of the fiber system of the corpus callosum. It is at present impossible to refer the different forms of aphasia and apraxia to definite lesions in the brain, but careful study of the residual symptoms and of those that are temporary, with minute consideration of the related and general symptoms will help toward a better understanding of the relation of the different parts of the cerebrum to the speech functions. At present we know little regarding the normal physiology of the nerve processes as compared with our anatomical knowledge and we must have more information on the functional side of the associational processes before we shall have an understanding of the complex associations which may be called aphasia, or *asemia*, *asymboly*, *apraxia*, etc.

From both the scientific and the social sides the two congresses were very

valuable. At both congresses special bronze medals were given to each member, at Heidelberg one from the Grand Duke of Baden with the portrait of HELMHOLTZ, and at Amsterdam one with the portrait of the Queen. The social part of both congresses was well conducted, and the short résumés of papers that are given above can do no more than indicate the diversity and interest of the full programs in both series of meetings. In Heidelberg many of the papers were chemical in character and not of special interest to comparative or human neurologists. In Amsterdam there were some few psychological papers and discussions, and one section was devoted to the consideration of questions dealing with the care of the insane. It is expected that the proceedings of the congress of psychiatry, neurology, psychology and the care of the insane will be published, but there will be no official report of the proceedings of the congress of physiologists.

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THE ARCHITECTURAL RELATIONS OF THE AFFERENT ELEMENTS ENTERING INTO THE FORMATION OF THE SPINAL NERVES.

BY

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WITH ONE FIGURE.

INTRODUCTION.

Some rather surprising observations are recorded in a paper recently published on "Retrograde degeneration in the spinal nerves" (RANSON '06).

It was found that after the division of a nerve, containing 1500 medullated afferent fibers, there occurred a complete degeneration of 4500 spinal ganglion cells and that this was accompanied by little or no degeneration of the dorsal roots. It was at once apparent that these results would be very difficult to explain on the basis of the usual conception of the spinal ganglion. Accordingly, the literature dealing with the architecture of the spinal nerves and of their dorsal root ganglia has been carefully reviewed in the hope of finding some observations that would be of assistance in interpreting these facts.

Another reason for presenting the normal relation of the sensory elements of the spinal nerves is the fact that in order to obtain a norm for the second cervical nerve of the white rat (the nerve studied in this series of experiments) it was necessary to make a study of the numerical relations in that nerve and these observations have some value from the anatomical point of view.

This work was begun under the direction of Dr. H. H. DONALDSON, to whom the writer is indebted for many suggestions.

THE SPINAL GANGLION.

I. The distinction between the large and the small cells and the functional significance of the two forms.—It has long been known that there exist in the spinal ganglion two well marked types of cells, which differ from each other both in size and staining reaction. As early as 1886 v. LENHOSSÉK made a careful study of the small cells and expressed an opinion concerning their functional sig-

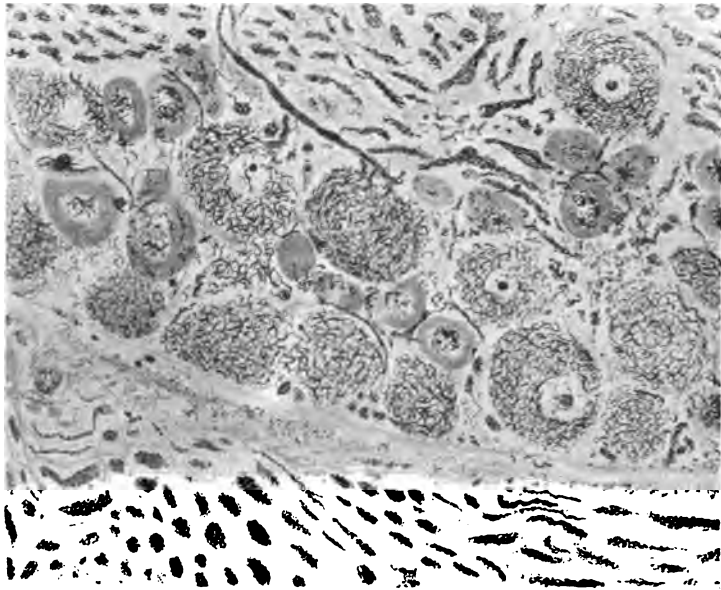


FIG. 1. The drawing represents a section $.5\mu$ thick from a spinal ganglion of a white rat, prepared by a modification of DONAGGIO's Method VII, Zeiss, ocular 4, Objective $\frac{1}{2}$.

nificance. According to his description, which relates in this instance to the spinal ganglion of the frog, these cells are very small, sometimes not more than 5μ in diameter; they are often angular and possess a relatively small amount of cytoplasm surrounding a large nucleus. In 1895 he adds to the previous description that the small cells are characterized not only by their size

but also by the fact that they stain more intensely with the diffuse protoplasmic dyes. Among those who have confirmed these observations of v. LENHOSSÉK may be mentioned FLEMMING ('95) and COX ('98). These small cells correspond to LUGARO's Type III and HATAI's Type II.

In connection with another investigation the writer has obtained preparations of the spinal ganglion by a slight modification of DONAGGIO's Method VII¹ (DONAGGIO '04) which demonstrate in a very striking manner a difference, probably chemical but possibly structural, between the large and the small cells. Since no other method presents so marked a contrast between the two cell types it is worth while to note the peculiarities of these preparations (see Fig. 1). The large cells present an absolutely colorless cytoplasm, throughout which there is a network of deep blue threads. These are largely absent from the nucleus. The small cells, on the contrary, present a cytoplasm of a deep violet which is almost entirely free from the blue threads, while the nucleus contains them in abundance. These same threads are seen in the axis cylinders. After a careful study of the literature it has not been possible to identify these threads with any known structure; but since the granular reticulum of CAJAL, the NISSL-bodies, the GOLGI-intracellular-net, the canals of HOLMGREN, the neurofibrils of BETHE and the still different fibrils of DONAGGIO and CAJAL together with the remaining protoplasm and the nucleus must occupy nearly all the space in one small cell, it does not seem probable that the threads just described are new structures. There can be no question however concerning the clear distinction which these preparations show between the large and the small cells, since the difference is a constant one and the picture is always the same. The distinction so strongly emphasized in these preparations is probably a chemical one and has its counterpart in the functional differences about to be mentioned. It should be noticed that there is a certain number of transitional cells which partake of the qualities of both large and small cells and are usually of medium size. Several are represented in the

¹ DONAGGIO's *Method VII (modified)*.—Pieces 2 to 3 mm. in thickness are fixed for 24 hours in a saturated solution of mercuric chloride in 10 per cent formalin to which has been added 1 per cent of glacial acetic acid; iodine-water 24 hours; distilled water 2 hours; pyridine 48 hours (change once); distilled water 24 hours; ammonium molybdate 24 hours; distilled water 1 hour; pyridine 48 hours (change once); an aqueous solution of thionin 1:5000, prepared at least two weeks previously (change once and stain for 48 hours); dehydrate and embed in paraffine; cut sections 5 to 7 μ thick.

drawing; they correspond to HATAI's Type III. These intermediate cells represent the stages through which the small cells pass while developing into the larger ones, a process which, as we shall see, is constantly going on in the growing animal.

RAWITZ ('80), in studying the spinal ganglia of various animals, had his attention drawn to these small deeply staining cells and came to the conclusion that they were young developing ganglion cells, the immediate result of a supposed—but confessedly undemonstrated—cell division. As proof he advances his observations that they are seldom found in the grown animal, but, on the contrary, are relatively frequent in the young. VON LENHOSSÉK ('86) does not agree with these statements of RAWITZ, for, while he admits that these cells are found more abundantly in young than in adult animals, he has also found them in large numbers in the full grown frogs. "I believe," says v. LENHOSSÉK, "that one may account for the presence of these little cells through the following consistent explanation: while, in the course of embryological development, the majority of ganglion cells become very much enlarged, a part of them as well as their associated nerve fibers stop at lower stages of development; such undeveloped nerve cells represent the little cells under discussion. According to this conception the cells in question would not be young and capable of further development, but represent ganglion cells remaining permanently at primitive stages of evolution." In 1895 v. LENHOSSÉK returned to the subject of the significance of the small cells. "It is not superfluous to insist that the smaller cells, even indeed the smallest cells, are not to be regarded as functionless rudimentary structures, but as elements which just as truly as the large cells are functional parts of the nervous mechanism: we find them associated just like the large cells with a process which divides in the typical way" into a central and a peripheral fiber. "Still less is it justifiable to look upon them as young elements still undergoing development. We are dealing here therefore not with cells which will further divide or otherwise develop but with cells which are formed small once for all."

Evidence, to be presented in a succeeding paragraph, supports v. LENHOSSÉK in his contention that the small cells are not young in the sense of RAWITZ; but that all, large and small alike, being derived from a cell division at an early embryonic period,

may be designated as old. It would seem, however, that the point concerning their incapacity for further development is not so well taken. We will return to these points in another paragraph, and will now consider BÜHLER's conception of the *raison d'être* of the small cells.

BÜHLER ('98) noticed that under physiological conditions in the toad, the frog and the rabbit there occurred a degeneration of a few isolated large ganglion cells, which were however not described. The degeneration is, to all appearances, not very rapid; in a spinal ganglion of a frog about 20 or 25 at a time, in rabbits relatively much fewer. He assumes that these disappearing ganglion cells are recruited from the ranks of the small cells, which develop into large cells as they are needed. "Since after the earliest stages a proliferation of ganglion cells no longer occurs, in order to remain capable of functioning throughout the period of life, the spinal ganglion must receive for its portion in the anlage sufficient reserve material in the form of undeveloped cells." HATAI ('02) has argued against this assumption on the ground that the number of spinal ganglion cells is approximately constant throughout the life of the individual. However the recent observations of KÖSTER on the spinal ganglia of cats, dogs and rabbits give some support to BÜHLER's statement (KÖSTER '03; p. 1098). "One recognizes, in every section of a normal ganglion, cells with all possible appearances of degeneration. One can see cells with eccentric swollen or fragmented nuclei, coarse and fine chromolysis, and all the changes which one may look upon as the reactional manifestations of the cells to the physiological degeneration found by SIGMUND MAYER in the peripheral nerves. We can, therefore, speak of a physiological degeneration of nerve cells." From these observations it would seem not impossible that a certain very slight amount of degeneration is going on constantly in the normal ganglion; and the question, whether or no the small cells are, as BÜHLER assumes, capable of replacing the cells lost in this way, is a question worthy of some consideration.

HATAI ('00) has given some attention to the significance of the small darkly staining elements, which with their scanty cytoplasm and large nuclei present many of the characters of embryonic cells, and concludes that they are "in a growing state or in a more or less permanently immature condition." In order to test this assumption he ('02) counted the number of large and

small cells in the spinal ganglia of the VI C., IV T., and II L. nerves of four white rats, ranging in weight from ten to one hundred sixty-seven grams, and found that, while the total number of cells in each ganglion remained approximately constant, there was a constant increase in the number of large cells and a corresponding decrease in the number of the small cells. This can only mean that the small cells are developing into large ones, and that therefore a considerable number of the former retain their capacity for development at least during the growing period.

It is of interest to note in this connection the observations made by HODGE ('89) that after electrical stimulation of nerves it is chiefly the large cells in the associated spinal ganglia that show the effect of fatigue. Considering all the cells large which have one diameter 50μ or over and those small which have not, a count gives the following results:

TABLE I.
Effect of Stimulating Ganglion Cells (HODGE).

IN 100 LARGE CELLS, NUCLEI			IN 100 SMALL CELLS, NUCLEI	
SHRUNKEN.	NORMAL.		SHRUNKEN.	NORMAL.
5	95	Resting	0	100
94	6	Stimulated	8	92

HODGE did not attempt an explanation of these interesting results; but in the light of the preceding discussion there seems to be little room for doubt that these small unworked elements are the immature cells of HATAI.

In summing up this discussion concerning the functional significance of the small cells of the spinal ganglion, it may be said that the absence of mitosis in the spinal ganglia during extra-uterine life excludes the possibility of their being young cells in the sense of RAWITZ. No more acceptable is the view of v. LENHOSSÉK that they are elements, the development of which has been permanently arrested; we must rather agree with HATAI that they retain for a long time their capacity for development, that, in fact, some of them are always in the process of transformation throughout the growing period of the animal. During the time that they are still undeveloped they do not show fatigue when the nerve is stimulated electrically. It is not yet satisfactorily determined whether they may serve as reserve cells capable of replacing the mature neurones destroyed by trauma or disease.

2. *Classification of the spinal ganglion cells according to the number and character of their processes.*—Since in this paper we are not directly concerned with the form of the spinal ganglion cells, we need only mention the most important points under this heading. That the cells of the spinal ganglion were all associated with a single T-shaped process was the accepted view until 1896, when DOGIEL published his important work on the form of the elements in the spinal ganglion. To DOGIEL belongs the credit of having first clearly differentiated the following cells in the spinal ganglia of mammals.

A. Unipolar cells. Type I. The well known unipolar cells, both large and small, with the typical T-shaped processes of RANVIER.

Type II. A new form first seen by DOGIEL, the single process of which breaks up into numerous fine branches that end in pericellular baskets within the ganglion itself.

B. Bipolar cells—very few, only one or two in each ganglion.

C. Multipolar cells with two nerve processes, one centrally, the other peripherally directed, and many dendritic processes arising from the angles of the irregularly shaped cell body. These dendrites penetrate the capsule and end among the cells of the ganglion.

The observations of DOGIEL were made upon preparations stained by his modification of the methylene blue technique. More recently ('05) CAJAL has published a preliminary account of his studies on the spinal ganglion with his new silver method. One of his cell-types is distinctly new and may be described here since it serves to emphasize the wealth of connections within the ganglion. This is an unipolar cell, possessed of very fine dendrites which take origin, sometimes from the surface of the cell itself, sometimes from the origin of the axis cylinder. These dendrites gradually enlarge and terminate in spheres, encircled by an entire system of concentric capsules. These dendrites sometimes bifurcate and give rise to a pair or more of terminal globes. He distinguishes two varieties among these cells: in one the terminal spheres are found beneath the capsule of the cell of origin and are in relation with the pericellular "nests" of CAJAL and DOGIEL, in the other the terminal globes are lodged in the intercellular spaces sometimes far distant from their point of origin.

We return now to a point more directly in keeping with the general purpose of this paper, namely, to the form of the small cells. HATAI ('01), apparently quoting from DOGIEL, says that "the number of these cells from which no axon can be traced is large." HARDESTY ('05) agrees that "a larger portion of these extra cells belong probably to the anaxonic type of neurone, latent cells which have not yet developed processes." Both HATAI and HARDESTY had in mind only the fact that the small cells were not connected with medullated fibers in the dorsal root or peripheral nerve—a fact which stands uncontested—but the conclusion that these cells are necessarily anaxonic is unnecessary and misleading. I have not been able to verify the citation from DOGIEL, and there seems every reason to believe that instead of being numerous such apolar cells do not occur at all in the spinal ganglion. In his extremely careful study of these structures, which lead him to insist on the presence of bipolar and multipolar cells, although never more than two or three such were found in one ganglion, DOGIEL does not mention the presence of these "anaxonic neurones." On the other hand, he describes in detail the single process of the small cell as being a typical T-shaped process with two branches, one directed toward the spinal cord, the other toward the periphery. These processes are usually destitute of myelin, but a few are medullated for a part of their course. He was able to trace these non-medullated processes of the small cells into the dorsal roots and into the peripheral nerves as far as the junction of the afferent and efferent fibers.

The absence of apolar cells is again the implication of v. LENHOSSÉK in the quotation already given. "We find them (the small cells) just as truly as the large cells associated with a process which divides in a typical way." But v. LENHOSSÉK does not leave the question in this obscure way, but says, in another place (*Bau des Nervensystems*, p. 268), "If we study the spinal ganglion of one of the more highly developed vertebrates or even the frog with suitable isolation, teasing or staining methods, we find in it, in addition to the interstitial connective tissue, blood vessels and nerve fibers, also numerous nerve cells of varying size of which the typical form is unipolar. *There are no apolar cells.*"

We have also to note the negative findings of HODGE ('89), who, having obtained physiological results that lead him to expect large numbers of apolar cells in the spinal ganglia of frogs, under-

took to demonstrate their presence in teased preparations but came to the conclusion that "Apolar cells do not occur in the spinal ganglia of frogs in any considerable numbers, none having been found."

3. *Interrelations among the spinal ganglion cells*.—The spinal ganglion is not to be regarded as an aggregation of more or less spherical cells each independent of the others and connected only with its central and peripheral processes; but is in reality a complicated mass containing the ramifications of dendrites and axis cylinders, forming exceedingly intricate intercellular meshworks and pericellular baskets, the cells in this way being brought into close functional relations with each other. Moreover there are sympathetic fibers which enter the ganglion via the ramus communicans to join in the formation of these baskets.

ARONSON ('86) was the first to describe the pericellular baskets in the spinal ganglion and his observations were confirmed by CAJAL ('90). The latter investigator regarded them as ramifications of fibers from the sympathetic system. It was DOGIEL however who first cleared up our notions on this point by describing a variety of cell ("Type II") which has for its sole function the establishment of intraganglionic connections.

SPIRLAS ('95) called attention to the existence of collaterals arising from the processes of the embryonic spinal ganglion cells. The observations were confirmed upon adult material by DOGIEL in 1896: "from the processes of many large and small ganglion cells, before their division into two fibers, one, two or three collaterals of varying thickness are given off which at a greater or less distance from their cells break up into fine threads." LEVI ('05) has followed the embryological formation of these collaterals.

In 1896 HUBER described a variety of spinal ganglion cell from the axon of which recurrent collaterals are given off. These run back and end in disks upon the cell from which the axon arose.

Still another means of intercommunication between the spinal ganglion cells is found in the dendritic processes of the multipolar cells and the more numerous unipolar cells of CAJAL, possessing fine dendritic branches with spherical endings which may either be in connection with the immediate pericellular basket or may run for considerable distances in the intercellular spaces to make connections in other parts of the ganglion.

Expressed in other words, the relations are as follows. Sym-

pathetic fibers enter the ganglion and break up about the cells, especially those of DOGIEL's Type II. The single processes of these cells of DOGIEL break up within the ganglion into a multitude of little twigs which form baskets about still other cells, while the stem process of many of the latter, i. e., the ordinary spinal ganglion cells, gives off delicate collaterals, which also take part in the formation of the fiber complex of the ganglion. All this wealth of axonic ramifications, together with the dendritic branches of some of the cells, forms a basis of intercommunication which argues for a close functional relationship among the individual spinal ganglion cells.

THE DORSAL ROOTS.

1. *The relation of the fibers of the dorsal roots to the cells in the substantia grisea of the spinal cord. Examination of NISSL's view that they are axons of such cells.*—A very peculiar observation noted in a paper recently published on "Retrograde Degeneration" (RANSON '06), namely, that after half of the spinal ganglion cells have disappeared as the result of section of the associated nerve, there are to be found in the dorsal root very nearly if not quite the normal number of fibers—and all this according to careful counts made on a considerable number of animals—has led to a careful consideration of NISSL's ('03) recently published conception of the dorsal roots, as a possible though improbable explanation of these results. Had the idea that the dorsal root fibers are independent of the spinal ganglion cells been advocated by any lesser authority we might indeed pass it by as unthinkable; but we cannot so lightly treat a statement by FRANZ NISSL. According to him ('03, p. 334), "The posterior root fibers are united with the cells of the spinal cord and especially with the cells of the substantia gelatinosa and only pass through the ganglion; and . . . the cells of the spinal ganglion also send fibers toward the periphery." The facts on which he bases this remarkable assertion are that after section of the posterior roots the cells of the spinal ganglia do not show change, while certain cells in the spinal cord, especially the cells of the substantia gelatinosa, undergo chromatolysis and even complete degeneration. It may be said however that, while true axonal reaction does not occur after section of the root, yet very considerable changes are induced in the ganglion cells

(KLEIST and KÖSTER); and there are plenty of cases of degeneration in neurone chains similar to the disappearance of the cells of the substantia gelatinosa—e. g., the degeneration of the motor cells with their peripheral motor fibers after section of the dorsal roots (BRAEUNIG '03). He also cites, as bearing on this point, the anomalous trigeminus found by v. GUDDEN in a calf, which showed no sensory root fibers. The ganglion itself was normal, as were also the fibers of the peripheral nerve arising from it, although these peripheral fibers were greatly decreased in number. According to NISSL's view the fibers whose cells were located within the brain had failed to develop, while those whose cells were located in the Gasserian ganglion had developed normally.

It would seem that these are rather insufficient grounds for revising our conception of the dorsal root, based as it is on such a large number of careful investigations; and it should be remembered, in this connection that those who have worked with the histology of the spinal ganglion, whether in teased preparations or GOLGI-material, have considered the dorsal root fibers identical with the central branches of RANVIER's T-fibers. Of the existence of some fibers in the dorsal root whose cells lie in the cord, there can be no doubt, at least so far as certain of the lower forms are concerned (CAJAL '90; v. LENHOSSÉK '90; and VAN GEHUCHTEN '93).

According to the experiments of JOSEPH ('87) on the second cervical nerve of the cat, these fibers are also found in mammals. After section of the dorsal root, he has observed that some fibers in the central portion remain normal and in the nerve a small number degenerate. At first opposed by SINGER and MÜNZER ('90), these results of JOSEPH have been confirmed by these same authors in a later paper ('95) and anticipated by the earlier work of KAHLER ('84).. KOPCZYNSKI ('06) has been unable to verify these observations.

It is to be borne in mind that, while these direct observations show the presence of fibers of passage in the spinal ganglion, they also indicate that only a few fibers are of this category and that these are efferent; and by no means do they support the view of NISSL that all the fibers of the dorsal root arise from cells situated in the spinal cord. And, as we shall see, the condition described in the paper on retrograde degeneration, namely, the presence of

a normal dorsal root associated with a ganglion which has lost one-half of its cells, is susceptible of another explanation than that suggested by NISSL's theory. All in all, then, while the evidence requires that we should be open-minded on this question, it is not sufficient to overthrow the belief that the dorsal roots are predominately composed of the central branches of RANVIER's T-processes. The evidence from the silver preparations, that one branch of the stem process of the spinal ganglion cell runs through the dorsal root, is very convincing. This evidence has been well summarized by VAN GEHUCHTEN ('92).

2. *Numerical relations between the spinal ganglion cells and the medullated fibers of the dorsal roots.*—FREUD ('78), working on Petromyzon, found a considerable excess of fibers in the dorsal roots over the cells in the spinal ganglion, due to the fact that the cell bodies of many of the afferent neurones are located in the spinal cord. HODGE ('89) counted the dorsal root fibers and the cells in the associated ganglion in the frog, and found about three cells for each fiber. BÜHLER ('98) has shown that the number of cells in the spinal ganglia increases as the test-animal is higher in the zoölogical series; least for fish, it is greatest in mammals. He also found that in the frog there were about five ganglion cells for each dorsal root fiber. GAULE and LEWIN ('96) found in the rabbit a ratio between cells and fibers of 6 to 1. HARDESTY ('05) found in the frog a ratio varying from 2.7 to 3.6 cells per fiber. HATAI ('02), working on the white rat, obtained the following results for the adult specimen of 167 grms. body weight.

TABLE II.

Ratio of Spinal Ganglion Cells to Dorsal Root Fibers (HATAI).

NERVE.	NUMBER OF CELLS.	NUMBER OF FIBERS.	RATIO.
VI C.....	12,200	4,227	1 : 2.8*
IV T.....	4,406	1,522	1 : 4.8*
II L.....	9,442	1,644	1 : 5.7

* The figures 2.7 and 4.3 given in the original are obviously misprints.

The writer, in studying the normal relations in the second cervical nerve of the white rat, has obtained results confirmatory of those of the authors already mentioned. In the three cases in which the dorsal root fibers and spinal ganglion cells were enu-

merated in the same individual nerve, a rather constant ratio of approximately 1 fiber to 3.2 cells was obtained. The first two specimens were 72 days old and weighed about 110 grams, the third was six months old and weighed 188 grams.

TABLE III.

Ratio of Spinal Ganglion Cells to Dorsal Root Fibers (RANSON).

SPECIMEN.	NUMBER OF CELLS.	NUMBER OF FIBERS.	CELLS PER FIBER.
72 days.....	7,721	2,472	3.1
72 days.....	8,116	2,394	3.3
6 month.s.....	8,624	2,689	3.2

The number of cells in a given spinal ganglion exceeds the number of medullated fibers in the corresponding root; this excess holds alike for frogs and mammals, although the actual percentage of the excess varies greatly. HATAI and HARDESTY ascribe to the anaxonic cells the responsibility for this condition; but, since we know that these cells do not exist in any appreciable number, we are thrown back upon the non-medullated fibers of the small cells as the chief source of the discrepancy. While it is possible that the majority of these non-medullated fibers do not push out into the dorsal root, it seems probable that the number of cells in the spinal ganglion does not exceed the number of axis cylinders in the dorsal root by so large a number as it does the number of myelin sheaths. A count of the dorsal root fibers obtained by a differential axis cylinder stain is the logical method of answering this question.

3. *The increase in the number of medullated fibers in the growing animal.*—HARDESTY ('05) has shown that, when his frogs were arranged in a series of increasing body weight, there was a general, though not very regular, increase in the number of fibers in the ventral and dorsal roots as well as in the peripheral nerves.

The white rat however in the hands of HATAI ('03) has given uniform results, showing a regular increase in the number of medullated fibers both in the ventral and dorsal roots.

The II C. nerve of the white rat shows more variability; in a general way however the number of fibers is increasing. The increase is, however, by no means as rapid, nor is there such a large number of fibers added as in the nerves studied by HATAI.

These observations are recorded in the accompanying table.

TABLE IV.

Rate of Medullation in the Second Cervical Nerve of the White Rat (RANSON).

AGE.	MEDULLATED FIBERS IN THE DORSAL ROOT.		MEDULLATED FIBERS IN THE VENTRAL ROOT.
12 days.....	1608		
12 days.....	1521		
12 days (average).....	—	1564.5	
72 days.....	2472		689
72 days.....	2394		660
72 days.....	1059		590
72 days.....	2217		591
72 days (average).....	—	2261	— 632.5
6 months.....	2891		773
6 months.....	2689		703
6 months (average).....	—	2790	— 736.5

THE NERVE.

1. *The proportion of sensory and motor fibers.*—All investigators have found a larger number of fibers in the dorsal than in the ventral root. According to INGBERT ('04) the ratio of all the motor and sensory fibers arising from the left side of the human spinal cord is 1 : 3.2, and from the second cervical segment alone 1 : 6. HATAI ('03) working with the C. VI, T. IV, and L. II nerves of the white rat finds an average ratio of 1 : 2.3. The normal relations in the C. II nerve of the white rat are expressed in the following table, representing the writer's enumeration of the ventral and dorsal root fibers for that nerve.

TABLE V.

Number of Ventral and Dorsal Root Fibers in the II C. Nerve of the White Rat (RANSON).

AGE.	VENTRAL ROOT.	DORSAL ROOT.	RATIO.
72 days (110 grms.).....	689	2,472	1 : 3.6
72 days (110 grms.).....	660	2,394	1 : 3.6
72 days (110 grms.).....	590	1,959	1 : 3.3
72 days (110 grms.).....	591	2,217	1 : 3.7

This table shows that the ventral root fibers are about 28 per cent as numerous as the dorsal root fibers.

2. *The distal excess.*—As has been said, considerably more sensory than motor fibers enter into the formation of the peripheral nerve. But, when we compare the sum of the fibers in the ventral and dorsal roots with the total number present on the distal side of the ganglion, we find a distinct excess on the distal side. The earlier investigators who undertook to compare the number of fibers on the two sides of the ganglion, either found them equal or

else the peripheral count so little in excess that they regarded it merely as a matter of technical error and attached no significance to it. Later, BIRGE ('82) found an excess of fibers on the peripheral side of the II C. ganglion of the frog amounting to 16 per cent; and BÜHLER ('98), also working on the frog, found in one nerve an excess of 25 per cent. HARDESTY ('99, '00, '05) has spoken of these extra fibers as the "distal excess" and found that it varied in the frog from 5 per cent to 61 per cent. GAULE and LEWIN ('96) found a distal excess in three of the sacral nerves of a rabbit of 19 per cent, 11 per cent, and 15 per cent, respectively. My observations on the II C. nerve of the white rat are confirmatory of these previous results. Here we have to do with a distal excess of 8 or 10 per cent. This is of interest since DALE ('00) found in coccygeal nerves of cats an average distal excess of only 0.63 per cent.

TABLE VI.

Showing the Distal Excess in the II C. Nerve of the Adult White Rat (RANSON).

WEIGHT.	VENTRAL ROOT.	DORSAL ROOT.	SUM OF ROOTS.	DISTAL EXCESS.	PERCENT- AGE OF D. E.	SUM OF RAMI.	VENTRAL RAMUS.	DORSAL RAMUS.
302 grms.	646	2386	3032	257	8	3289	887	2402
161 grms.	672	2090	2762	276	10	3098	708	2390

HARDESTY has made a careful study of the possible explanations of this distal excess. It is much too complicated a question for us to enter upon here. It can only be said in passing that there is evidence for the presence of medullated fibers of sympathetic origin which pass through the nerve to end in the ganglion and, hence, would not be found in either of the roots. There is also evidence that both sensory and motor fibers may bifurcate at the level of the ganglion. But after a careful consideration of all the possibilities, HARDESTY does not think any one cause sufficient to explain the facts and believes that several factors must operate together in the production of the distal excess. The idea of NISSL, discussed in a previous section, that the dorsal root fibers pass through the ganglion without making any connections and are there joined by others arising in the ganglion, would, if it should be found correct, offer an adequate explanation of the distal excess, especially of those cases where the excess is large and

amounts to more than 60 per cent, as in one case (HARDESTY '00) where 337 fibers on the proximal side were associated with 544 on the distal side of the ganglion. In those cases however, where the excess is not more than 5 per cent (2422 proximal to 2543 distal fibers, HARDESTY '05), the hypothesis of NISSEL would require that very few fibers originate in the ganglion.

3. *The presence of non-medullated fibers in the nerve.*—It has already been said that DOGIEL was able to trace the non-medullated fibers as far as the junction of the afferent and efferent roots. So important is this work of DOGIEL's that a full quotation may be given.

Ausser der Grösse besteht der einzige Unterschied zwischen den in Rede stehenden Zellen und den grossen Ganglienzellen darin, dass von einer jeden solchen Zelle immer nur ein einziger äusserst dünner und während seines ganzen Verlaufs myelinlos bleibender Fortsatz abgeht. Von der Zelle gewöhnlich in der Form eines kleinen Konus beginnend, bekommt der Hauptfortsatz das Aussehen eines äusserst dünnen, nicht selten varicösen Fadens, welcher noch unter der Zellkapsel, oder sofort nach dem Austritt aus ihr, 2-3 bogenförmige Biegungen macht, worauf er mehr oder weniger gradlinig oft eine sehr lange Strecke zurücklegt und sich endlich V- oder T-förmig in zwei dünne varicöse Fäserchen teilt. Soviel ich weiss, hat RETZIUS zuerst die Aufmerksamkeit auf das Vorkommen kleiner Ganglienzellen in den Spinalganglien der Säugetiere (Kaninchen) gelenkt, indem er sich über dieselben folgendermassen ausdrückt: "Im Gegenteil geht, besonders bei kleineren Ganglienzellen, oft von einer schwach abgeschnürten Stelle der Zelle ein blasser Ausläufer aus, welcher zuweilen sich auf weite Strecken verfolgen lässt und dabei die marklose Beschaffenheit behält; länglich-ovale Kerne treten in gewissen Entfernungen an ihm auf, und er wird allem Anscheine nach zu einer gewöhnlichen myelinfreien Nervenfasern; wie sich diese im späteren Verlaufe verhält, konnten wir nicht ergründen. Einmal sahen wir indessen diesen blassen Ausläufer sich dichtomisch teilen." Es ist mir gelungen diese Lücke in den Beobachtungen von RETZIUS auszufüllen und nachzuweisen, dass die Hauptfortsätze der kleinen Zellen und die aus ihrer Teilung hervorgehenden Fasern, soweit sie in den Ganglien und sogar in den hinteren Wurzeln und an deren Zusammentrittsstelle mit den vorderen Wurzeln zu verfolgen sind, überall den Charakter markloser Fasern bewahren, oder aber nur an einer gewissen Strecke von einer äusserst dünnen, früher oder später wieder verschwindenden Markhülle umgeben werden.

It is important to note in this connection that WEIGNER has recently shown that there is a considerable number of non-medullated fibers in the nervus intermedius; and this should lead to an examination of other cranial and spinal nerves to determine if non-medullated nerve fibers had not been overlooked in them.

It will be shown in my next paper that the small cells of the spinal ganglion, which DOGIEL says possess non-medullated fibers show typical axonal reaction after section of the peripheral nerve and that it is these small cells that degenerate and disappear, facts which can be explained only on the assumption that these non-medullated fibers extend into the peripheral nerve. The existence of these fibers and the degeneration of the small cells offers a satisfactory explanation of the results presented in the former paper on Retrograde Degeneration in the Spinal Nerves.

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THE NERVOUS SYSTEM OF THE AMERICAN LEOP-
ARD FROG, RANA PIPIENS, COMPARED WITH
THAT OF THE EUROPEAN FROGS, RANA ESCU-
LENTA AND RANA TEMPORARIA (FUSCA).

BY

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WITH SIX FIGURES.

With the advances which are being made in the correlation of function and structure, the need is felt on many sides for a more detailed, accurate and quantitative determination of the anatomical, physiological and chemical differences between closely related species, as well as between the same species from different localities.

The general notion of a physiological and chemical criterion for species has been discussed by DE VARIGNY ('99) and, although this is not the place to review the literature touching this topic, it is nevertheless appropriate to name CAMERANO's paper ('00) on the variation of the toad, which, among his many important contributions in this general field, is the one most closely related to the following investigation. Moreover, KELLCOTT's recent study of correlation and variation in internal and external characters in the common toad ('07) emphasizes relations which have a direct bearing on the interpretation of my own results.

In 1898 I made a study of the weight of the brain and of the spinal cord in the bull-frog *R. catesbiana* (DONALDSON '98). Two years later, in collaboration with Dr. D. M. SCHOEMAKER,

a similar series of observations on the leopard frog, *R. pipiens*,¹ was published (DONALDSON and SCHOEMAKER '00).

In 1902, utilizing the data in both of these investigations, I was able to show that the weight of the central nervous system in both of these species could be calculated by a formula based on the body weight and on the total length of the frog (DONALDSON '02).

For comparison with these results the observations of FUBINI ('81) on the European frogs were alone available.

An examination of FUBINI's tables, which are discussed in part in my paper of 1898, referred to above, showed that his findings were so irregular and so different from my own, that it was fair to conclude that he had not worked with sufficient care.

In order to test this conclusion, I obtained in the spring of 1898, through the courtesy of the Zoölogical Institute at Zurich, Switzerland, a series both of *R. esculenta* and *R. temporaria* (*fusca*), all the specimens having been fixed in formalin by a uniform method. A comparison of these specimens with the fresh *R. pipiens* on the one hand, and on the other with *R. pipiens* fixed by the same method, indicated that the central nervous system in *R. pipiens* was heavier than in the European species, and at the same time did not support any of the peculiar findings of FUBINI, such as the relatively great weight of the spinal cord. Nevertheless, limitations in the range in size of the Zurich series and the possibility that the European and American species were differently affected by the fixation treatment, led me to delay publication on this point until fresh material could be examined. The opportunity to do this came in the summer of 1904. In July of that year, through the courtesy of Professor SHERRINGTON, I was able to examine a series of *R. temporaria* (*fusca*) in the physiological laboratory of University College at Liverpool, England; and in August, through the courtesy of Professor GAULE, a corresponding series of *R. esculenta* was examined in the Physiological Institute of the University at Zurich, Switzerland.

In order to eliminate as far as possible, the influence of *season* on this comparison, Dr. HATAI examined for me, also in August, a series of *R. pipiens* in the Neurological laboratory of the Uni-

¹In previous papers on the leopard frog, published from my laboratory, this species has been designated as *Rana virescens brachycephala*, Cope. It now appears that this name is not correct, and that the species in question should be designated *Rana pipiens* (Schreber) as given above (DONALDSON, *Science*, vol. 26, p. 655, 1907.)

versity of Chicago. It is the results of these three series of observations which are now to be compared.

As the foregoing shows, this investigation was undertaken primarily to test the correctness of FUBINI's observations. It has resulted however in bringing to light several differences between the nervous systems of the species compared, and these differences seem worth recording. At the same time, FUBINI's observations have been found untrustworthy. This, however, is a matter of small importance, and the brief discussion of FUBINI's work will be deferred to an appendix.

Before presenting the data on the nervous system, it will be desirable to record some of the characters in which these three species of frogs closely resemble one another. The resemblances important for our present purpose are enumerated below:

- (1) In external appearance and shape; color markings excepted.
- (2) In the range in body weight (the heaviest specimens are always females).
- (3) In the ratio obtained by dividing the body weight by the total length, that is, the average amount of body weight for each running millimeter of total length.

It will be necessary to interrupt the enumeration for a moment in order to elaborate this point (3).

In the full tables are given the body weight and the total length of each individual examined. In the condensed Table 10, these same data are arranged to give the averages for *groups of three*. Thus for each species in the latter table there are four entries, and in each entry both the average body weight and the average total length are given. If the former be divided by the latter

$$\frac{\text{Body weight}}{\text{Total length}}$$

we obtain a number which represents the average amount of weight for each running millimeter. Since the increase in body weight is more rapid than the increase in total length, this value of course changes with the absolute weight of the frog, increasing as the frog becomes absolutely heavier. The values thus obtained are given in Table 1.

These values are better understood when thrown into a curve, as in Chart 1.

It appears from the chart that the curves are nearly parallel,

TABLE I.

	BODY WEIGHT IN GRAMS.	BODY WEIGHT PER MILLIME- TER IN GRAMS.
R. pipiens.....	14.9	.102
	23.2	.135
	30.8	.168
	43.2	.218
R. esculenta.....	15.9	.114
	22.0	.134
	35.0	.199
	40.2	.208
R. temporaria.....	15.9	.107
	23.1	.137
	28.0	.162
	31.3	.177

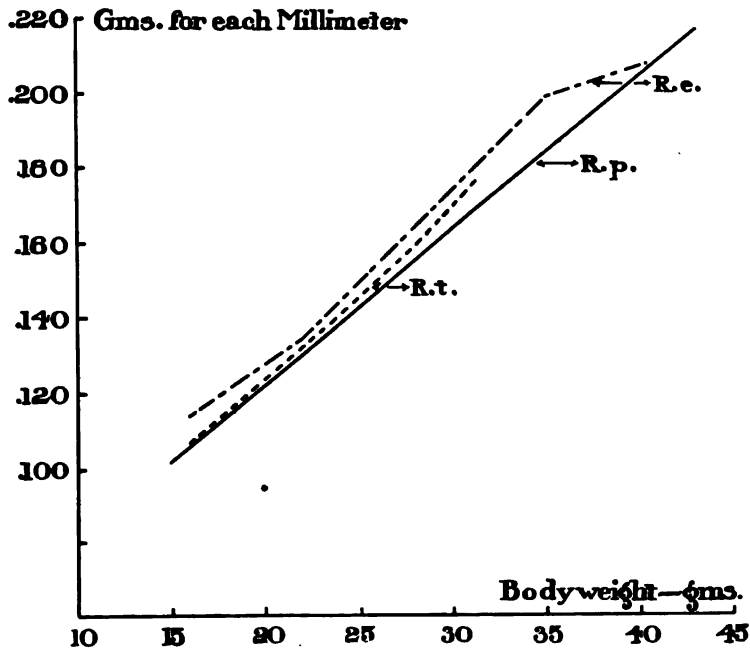


CHART 1.

Showing the average amount of body weight for each running millimeter of total length.

R. p. = Rana pipiens.

R. e. = Rana esculenta.

R. t. = Rana temporaria.

and that on the average, the lower figures differ only 4.1 per cent (*R. pipiens*) and 2.3 per cent (*R. temporaria*) respectively, from the highest figures, given by *R. esculenta*. The relation of body weight to total length is therefore nearly the same in all three species.

(4) In the fraction of the total length represented by the combined lengths of the leg bones.

Table 2 gives these figures in their final form.

TABLE 2.

Percentage of the total length represented by the combined lengths of the leg bones.

	No. of SPECIMENS.	
<i>R. pipiens</i>	12	68.7%
<i>R. esculenta</i>	5	70.7%
<i>R. temporaria</i>	6	69.4%

The percentages in the foregoing tables were obtained as follows: That for *R. pipiens* from an average of twelve records on individuals ranging from 14.85 to 42.54 grams in body weight (DONALDSON and SCHOEMAKER, '00, Table VII); that for *R. esculenta* from five specimens of the Zurich series of 1898, having a body weight of 12.3–20.4 grams; and that for *R. temporaria* (*fusca*) from six specimens of the same series ranging in body weight from 17.9–34.7 grams.

Table 2 serves to show that in this character the three species are nearly alike.

(5) In the proportional lengths of the several leg bones.

TABLE 3.

	No. of SPECIMENS.	FEMUR.	TIBIA.	FOOT (TARSUS AND PES).
<i>R. pipiens</i>	12	25.5%	29.3%	45.2%
<i>R. esculenta</i>	5	26.3%	28.2%	45.5%
<i>R. temporaria</i>	6	26.1%	28.7%	45.2%

The figures in Table 3 are based on the same data as were used for Table 2. For comparison in the case of *R. esculenta* however, we have in addition, the measurements from BOULENGER ('97). These are taken both from his tables and from measurements made on the bones as represented in his plates.

The data from BOULENGER give the following:

TABLE 4.

R. ESCULENTA.	No. OF SPECIMENS.	FEMUR.	TIBIA.	FOOT (TARSUS AND PES).
Variety <i>rabibunda</i>	1 M.+1 F.	26.7%	29.2%	44.1%
Variety <i>rabibunda</i>	1 F.*	27.7%	28.9%	43.4%
Variety <i>typica</i>	1 M.+1 F.	26.8%	27.3%	45.9%
Variety <i>lessonae</i>	1 M.+1 F.	25.9%	26.5%	47.6%

* Measured from Boulenger's Fig. 101, p. 280.

In my Zurich series the individual measurements correspond to those for the varieties *rabibunda* and *typica* as determined by BOULENGER. The average for these from the above table (4) is:

AVERAGE VALUES FOR VARIETIES *RABIBUNDA* AND *TYPICA*.

Femur	27.0
Tibia	28.3
Foot	44.7

And these values are close to those given for *R. esculenta* in Table 3.

For comparison in the case of *R. temporaria*, an average of two determinations, one male, one female, by BOULENGER is available. These give

Femur	25.6%
Tibia	28.4%
Foot	46.0%

which is in fair agreement with the values given in Table 3.

(6) In the relative length of the entire central nervous system (that is, the length of the brain plus the length of spinal cord), in relation to the total length of the frog.

This relation is of course not a constant one, because the total length of the frog increases more rapidly than the length of the entire nervous system. To make the comparisons, therefore, the percentages must be recorded in relation to the total length found for each individual or group. The data used in this determination were the following:

Ten (10) specimens of *R. pipiens* ranging in total length from 124 mm. to 185 mm. inclusive. The data being taken from the

research of DONALDSON and SCHOEMAKER ('00). These cases are averaged in groups of five.

Twelve (12) specimens of *R. pipiens*, these being the same as are given in Table 7 and averaged in groups of four (observations by Dr. HATAI). Both of the foregoing series of measurements were made on the fresh specimens.

Ten specimens of *R. pipiens*, after fixation in formalin, averaged in groups of five, and ranging in total length from 128-174 mm. This was the series used to control the measurements on the European frogs received from Zurich in 1898.

From the Zurich series of 1898, there were taken one group of five *esculenta*, ranging in total length, after fixation, from 128-170 mm., and also a series of fifteen *R. temporaria*, averaged in groups of five, and ranging in total length, after fixation, from 151 to 179 mm.

It seems fairest to tabulate the fresh, separately from the fixed material, so the first lot, entirely *R. pipiens*, is given in Table 5.

TABLE 5.

R. pipiens. Percentage values of length of the entire central nervous system, the total length of the frog being taken as the standard. Measurements on fresh specimens.

AVERAGES OF	TOTAL LENGTH MM.	PER CENT VALUE OF THE LENGTH OF ENTIRE CENTRAL NERVOUS SYSTEM.
4	150	17.2
5	153	17.8
5	175	17.2
4	177	16.2
4	196	16.3

TABLE 6.

Showing the same relation as Table 5. All measurements on material fixed in formalin.

SPECIES.	AVERAGE OF	TOTAL LENGTH MM.	PER CENT VALUE OF THE LENGTH OF THE ENTIRE CENTRAL NERVOUS SYSTEM.
<i>R. pipiens</i>	5	133	18.2
<i>R. esculenta</i>	5	145	17.9
<i>R. temporaria</i>	5	158	16.9
<i>R. temporaria</i>	5	166	16.2
<i>R. pipiens</i>	5	167	16.4
<i>R. temporaria</i>	5	173	16.0

Table 5 shows that the value in question ranges in the fresh specimens from 17.8 per cent to 16.2 per cent, and also tends to diminish as the total length of the frog increases. The same relations are shown in Table 6, in which all three species are represented, and these form as satisfactory a series as is given in Table 5.

We therefore conclude that in this character—the relative length of the entire central nervous system—the three species resemble one another closely.

It should be pointed out here that it follows from this that the smaller weight of nervous system which we find in the European forms (see below) must be associated with a diminution of one or both the transverse diameters, since the foregoing shows that it is not associated with variations in total length.

(9) In the arrangement of the main branches of the crural and sciatic nerves (DUNN '00 and '02). In the papers to which reference is here made, this point is fully discussed.

In view of the fact that the several species are similar in the foregoing characters, we might expect a high degree of similarity in the weight and structural relations of the central nervous system. Such however is not the case, and we turn therefore to a statement of the differences which have been observed.

The technique of weighing, measuring and dissecting, was uniform for the three species. This has already been described (DONALDSON, '98, DONALDSON and SCHOEMAKER, '00).

It may, however, be well to repeat here that the body weight was taken in a closed box; the weight of the contained ova being deducted from the body weight of the unopened specimen, in the case of the females. Also in both sexes correction was made for the stomach contents.

In taking the total length, the frog was suspended by the lower jaw, and the distance between the tip of the nose and the longest toe, the legs being fully extended, was measured with vernier calipers. The central nervous system was removed immediately after death, and the brain separated from the spinal cord by a section at the level of the tip of the calamus scriptorius. Both brain and cord were separated from their nerves by severing the latter at the points of their attachments to the central structures. To obtain the percentage of water, the material was dried for several days until it maintained a constant weight. For this a water bath ranging from 85° to 95° C. was used.

Although this is probably not the best method, it was uniformly applied in the case of all three series, so that the results are at least comparable, though the absolute values for the percentage of water may be open to question, until it has been shown that this material dried in vacuo, gives similar results.

Material examined.—The specimens of *R. pipiens* were 12 in number (10 males and 2 females) ranging in body weight from 11.6–47 grams. They were taken in the neighborhood of Chicago in the month of August, and examined between the twenty-third and thirty-first of August. For the data which are presented in Table 7 I am indebted to Dr. S. HATAI.

TABLE 7.
Data on *R. pipiens*.

BODY WEIGHT IN GRMS.	SEX.	TOTAL LENGTH IN MM.	WEIGHT IN GRAMS OF			RATIO OF BRAIN WEIGHT TO CORD WEIGHT.	PERCENTAGE OF WATER.	
			C. N. S.	BRAIN.	SP. C.		BRAIN.	SP. C.
11.6	M.	130	.0918	.0666	.0252	2.64	84.4	79.4
16.0	M.	150	.1148	.0796	.0352	2.26	85.2	80.7
17.0	F.	159	.1054	.0714	.0340	2.10	84.0	80.6
20.8	M.	170	.1232	.0844	.0388	2.17	85.2	81.6
22.5	M.	162	.1165	.0807	.0358	2.25	84.5	80.4
26.4	M.	180	.1372	.0946	.0426	2.22	84.4	78.4
27.6	F.	179	.1416	.1014	.0402	2.52	84.8	80.1
30.6	M.	180	.1454	.0998	.0456	2.18	84.6	79.8
34.2	M.	190	.1518	.1056	.0462	2.28	85.6	81.6
41.8	M.	197	.1652	.1146	.0506	2.26	86.9	82.2
43.9	M.	200	.1708	.1210	.0498	2.42	85.8	80.7
47.0	M.	198	.1664	.1140	.0524	2.17	84.4	80.5

The specimens of *R. esculenta* were eleven in number (3 males and 8 females) ranging in body weight from 12.4–45.03 grams. They were taken near Zurich on July 31, and were examined between August 1 and 5. The data are given in Table 8.

The specimens of *Rana temporaria* (*fusca*) were twelve in number (8 males and 4 females) ranging in body weights from 14.05–32.81 grams. They were taken near Liverpool shortly before July 11, and were examined July 11 and 12. The data are given in Table 9.

In all the foregoing series there is considerable individual variation in the characters observed, and so for the purposes of comparison, the complete tables have been condensed by taking the

averages for each three successive individuals, thus giving four entries in each of the condensed tables.

The only exception to this statement is in the case of *R. esculenta*, with but 11 records, and there the third entry in the con-

TABLE 8.
Data on *R. esculenta*.

BODY WEIGHT IN GRMS.	SEX	TOTAL LENGTH IN MM.	WEIGHT IN GRAMS OF			RATIO OF BRAIN WEIGHT TO CORD WEIGHT.	PERCENTAGE OF WATER	
			C. N. S.	BRAIN.	SP. C.		BRAIN.	SP. C.
12.40	F.	131	.0818	.0577	.0241	2.39	84.2	78.4
16.75	F.	144	.0926	.0634	.0292	2.17	83.4	79.1
18.43	F.	144	.0928	.0650	.0278	2.34	83.2	78.2
20.00	F.	161	.1103	.0756	.0347	2.17	82.5	79.2
22.00	F.	164	.1107	.0769	.0338	2.27	84.0	79.0
24.10	M.	167	.1217	.0841	.0376	2.23	83.4	78.4
33.85	M.	175	.1327	.0895	.0432	2.07	83.2	78.2
36.30	M.	177	.1478	.1004	.0474	2.11	83.4	78.6
37.56	F.	188	.1490	.0993	.0497	1.99	82.9	78.8
37.96	F.	194	.1427	.0953	.0474	2.01	82.8	77.8
45.03	F.	196	.1578	.1078	.0500	2.15	83.9	78.4

TABLE 9.
Data on *R. temporaria*.

BODY WEIGHT IN GRMS.	SEX	TOTAL LENGTH IN MM.	WEIGHT IN GRAMS OF			RATIO OF BRAIN WEIGHT TO CORD WEIGHT.	PERCENTAGE OF WATER	
			C. N. S.	BRAIN.	SP. C.		BRAIN.	SP. C.
14.05	F.	144	.0881	.0596	.0285	2.09	82.3	78.2
16.10	F.	151	.0991	.0690	.0301	2.22	82.7	79.0
17.65	M.	154	.0916	.0618	.0298	2.07	83.0	78.5
21.75	M.	171	.1045	.0671	.0374	1.79	82.8	78.2
23.45	M.	162	.0947	.0628	.0319	1.96	82.1	77.0
24.17	F.	173	.1333	.0864	.0469	1.84	81.9	76.5
27.05	M.	173	.1298	.0874	.0424	2.06	82.4	77.1
28.15	M.	168	.1018	.0687	.0331	2.07	82.5	76.7
28.95	M.	174	.1324	.0813	.0511	1.59	81.3	76.8
28.95	M.	178	.1485	.0928	.0557	1.66	81.3	76.8
32.15	M.	173	.1321	.0890	.0431	2.06	80.9	78.6
32.81	F.	178	.1161	.0766	.0396	1.93	82.7	78.0

densed tables is based on only two individuals, numbers 7 and 8 in the series. The condensed tables are given in connection with each character discussed. That for the weight of the entire central nervous system follows:

TABLE 10.

Weight of the central nervous system in grams, averages from groups of three.

	BODY WEIGHT	WEIGHT OF CEN- TRAL NERVOUS SYSTEM.	TOTAL LENGTHS IN MM.
R. <i>pipiens</i>	14.9	.1040	146
	23.2	.1256	171
	30.8	.1463	183
	43.2	.1674	198
R. <i>esculenta</i>	15.9	.0890	139
	22.6	.1142	164
	35.0	.1402	176
	40.2	.1498	193
R. <i>temporaria</i>	15.9	.0929	149
	23.1	.1108	167
	28.0	.1213	173
	31.3	.1323	176

The data in the foregoing tables are also presented in Chart 2 and the relations are more easily discussed by reference to the chart, which shows *R. pipiens* to have the heaviest central nervous system, *R. esculenta* the next heaviest, and *R. temporaria* the lightest.

By measuring the differences between the several entries for the two European species, and the corresponding points on the curve for *R. pipiens*, which is taken as the standard, it appears that on the average, the central nervous system of *R. esculenta* weighs about 89 per cent, and that of *R. temporaria* 88 per cent, of that found in *R. pipiens*.

It is known that dry air and starvation (DONALDSON '98, DONALDSON and SCHOEMAKER '00) tend to reduce the weight of the living frog, and probably of the central nervous system, also that the weight of the latter is increased in frogs which are moribund, and have consequently taken up an excessive amount of water.

There is no reason to think however that the foregoing observations are seriously modified by any of these influences.

Moreover unpublished observations on *R. pipiens*, in my possession, indicate a variation in the weight of the central nervous system with season. Nevertheless from the middle of June to the middle of September, such variations as occur, are hardly

significant, and the observations here used were made within fifty-one days (July 11 to August 31) and fall within the general

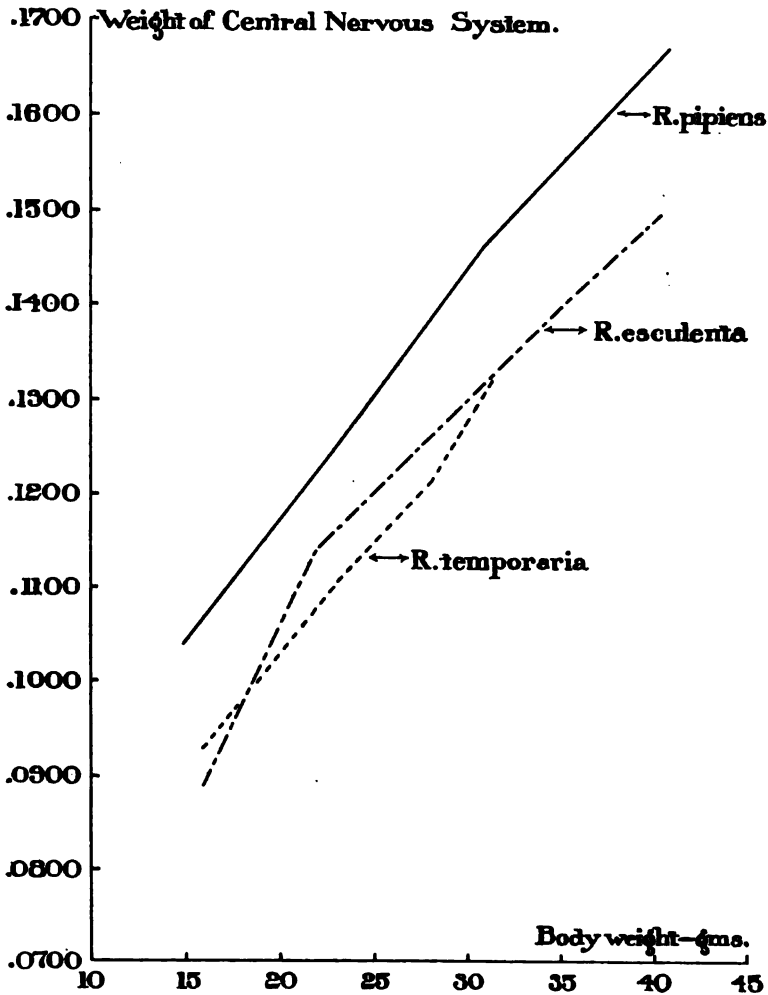


CHART 2.
Showing the weight of the entire central nervous system.

seasonal limits for constancy, as given above. This summer period is moreover the one during which the central nervous system shows its greatest weight. At the same time it is worthy

of note that the results obtained on *R. pipiens* in August, 1904, correspond with the *lowest* weights found during August, 1901, in the case of the unpublished series.

In one sense this is perhaps fortunate, because it shows that the values here reported for *R. pipiens* are minimal, and if those for the European forms are also minimal, then the differences are approximately normal. If, on the other hand, the values for the European species are higher than the minimal, then the differences here given are less than they should be. In any case, and this is the main point, it follows that the differences here given are not exaggerated. I conclude therefore that the European species have a central nervous system which weighs from 11 per cent to 12 per cent less than that of *R. pipiens*.

As the Chart 2 shows, the curves for the weight of the central nervous system run nearly parallel, and as in a previous study (DONALDSON '02) *R. pipiens* has been found to conform to the formula for the determination of this weight, which is based on the body weight and total length of the frog, it follows that the European species would also conform to this same formula.

The formula contains a constant, *C.*, which is different for each species, and which is modified by the general condition of any series. In the series of *R. pipiens* of 1902, the value of the constant *C.* was 28. In the present series of *R. pipiens* which, as has been noted, yields a low weight for the central nervous system, the value of *C.* is 26, and we should anticipate that it would be less for the two European species.

On making the calculations, I find the following values for *C.*

<i>R. pipiens</i>	<i>C</i> = 26
<i>R. esculenta</i>	<i>C</i> = 24
<i>R. temporaria</i>	<i>C</i> = 23

Our expectation then that the formula for the European species would have smaller values of *C.* is shown to be warranted.

On separating the weight of the brain from that of the spinal cord, and recording them separately, we have the relations given in Table 11.

Presenting these results in a form of a chart (Chart 3) it is seen that the brain weights for the several species follow the same order as that of the weight of the entire central nervous system, the superiority of *R. pipiens* being even more marked. The weights for the spinal cords however run much closer together.

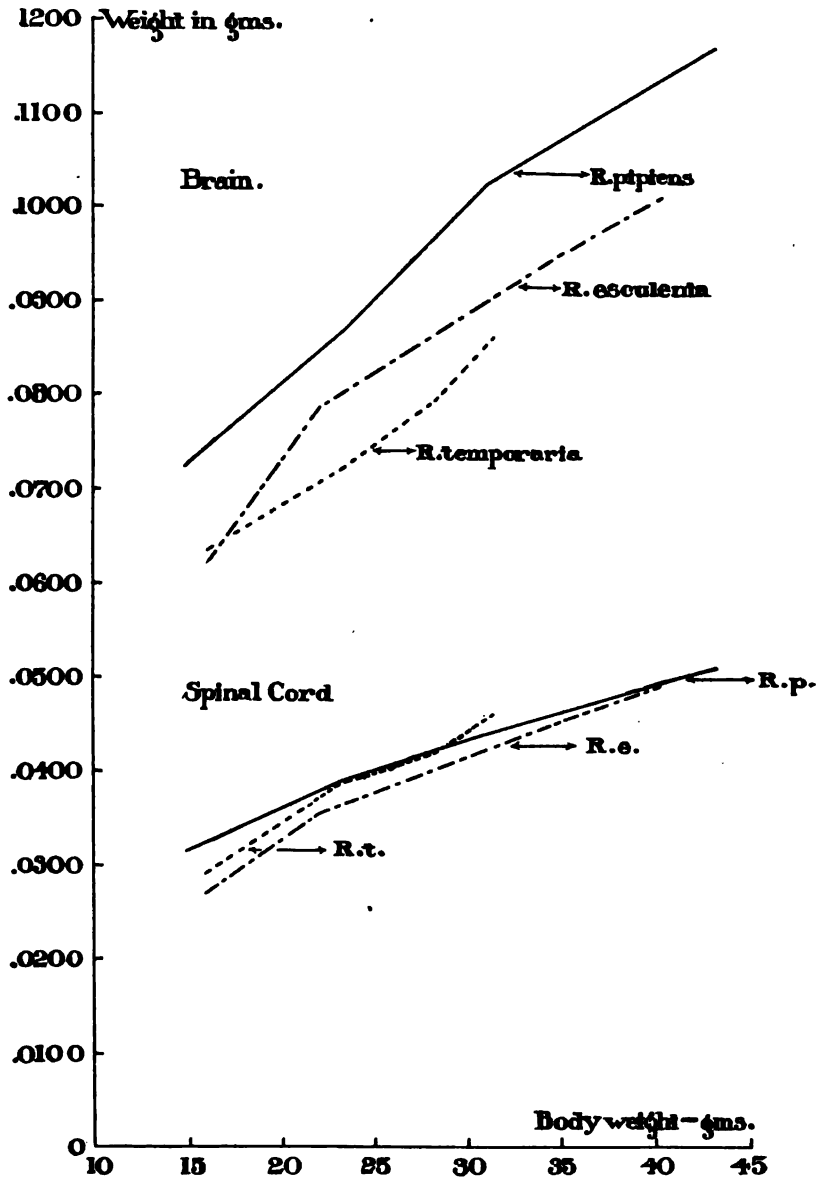


CHART 3.

Showing the weight of the brain and of the spinal cord.

R. pipiens has still the heaviest cord, but *R. temporaria*, with the lightest entire central nervous system, has a spinal cord nearly as heavy as that of *R. pipiens*, while the cord in *Rana esculenta* is distinctly lighter than in the other two species, having on the average 94 per cent of the weight of the cord in *R. pipiens*.

TABLE 11.
Weight of the brain and spinal cord in grams. Averages from groups of three.

	BODY WEIGHT.	BRAIN.	SPINAL CORD.
<i>R. pipiens</i>	14.9	.0725	.0315
	23.2	.0866	.0390
	30.8	.1023	.0440
	43.2	.1165	.0509
<i>R. esculenta</i>	15.9	.0620	.0270
	22.0	.0788	.0354
	35.0	.0949	.0453
	40.2	.1008	.0490
<i>R. temporaria</i>	15.9	.0635	.0294
	23.1	.0721	.0387
	28.0	.0791	.0422
	31.3	.0862	.0461

To show the relative weight of the brain as compared with that of the cord in these three species, we may use the ratio obtained by dividing the brain weight by the cord weight. These ratios are given in the following table:

TABLE 12.
Ratios of the weight of the brain to the weight of the spinal cord. Averages from groups of three.

	BODY WEIGHT.	RATIO.
<i>R. pipiens</i>	14.9	2.33
	23.2	2.22
	30.8	2.32
	43.2	2.28
<i>R. esculenta</i>	15.9	2.29
	22.0	2.22
	35.0	2.09
	40.2	2.05
<i>R. temporaria</i>	15.9	2.15
	23.1	1.86
	28.0	1.87
	31.3	1.87

Putting these data in the form of curves in Chart 4, we see that the relative brain weights follow the order of the absolute weights of the entire nervous system and of the brain, the highest ratios being given by *R. pipiens*.

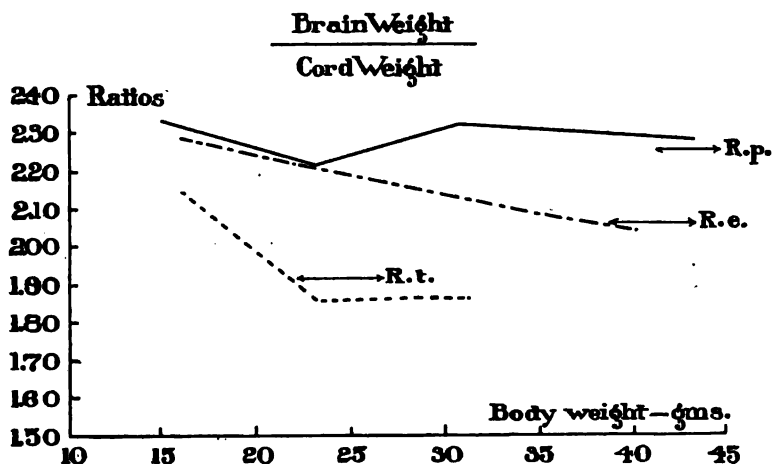


CHART 4.
Showing the ratios of brain weight to spinal cord weight.
R. p. = *Rana pipiens*.
R. e. = *Rana esculenta*.
R. t. = *Rana temporaria*.

TABLE 13.
Showing the percentage of water in the brain and in the spinal cord. Averages from groups of three.

	BODY WEIGHT.	PERCENTAGE OF WATER IN	
		BRAIN.	SPINAL CORD.
<i>R. pipiens</i>	14.9	84.5	80.2
	23.2	84.7	80.1
	30.8	85.0	80.5
	43.2	85.7	81.2
<i>R. esculenta</i>	15.9	83.6	78.6
	22.0	83.3	78.9
	35.0	83.3	78.4
	40.2	83.2	78.3
<i>R. temporaria</i>	15.9	82.7	78.6
	23.1	82.3	77.2
	28.0	82.1	76.9
	31.3	81.6	77.8

In addition to the several weights, a determination of the percentage of water was made in the case of both the brain and spinal cord. The method has been described already on p. 128.

The condensed results are given in Table 13.

On putting the data in Table 13 in the form of curves (Chart 5) it becomes evident at a glance that the percentages found in the three species are different, and also that they follow the order of the weight of the entire central nervous system and of the brain.

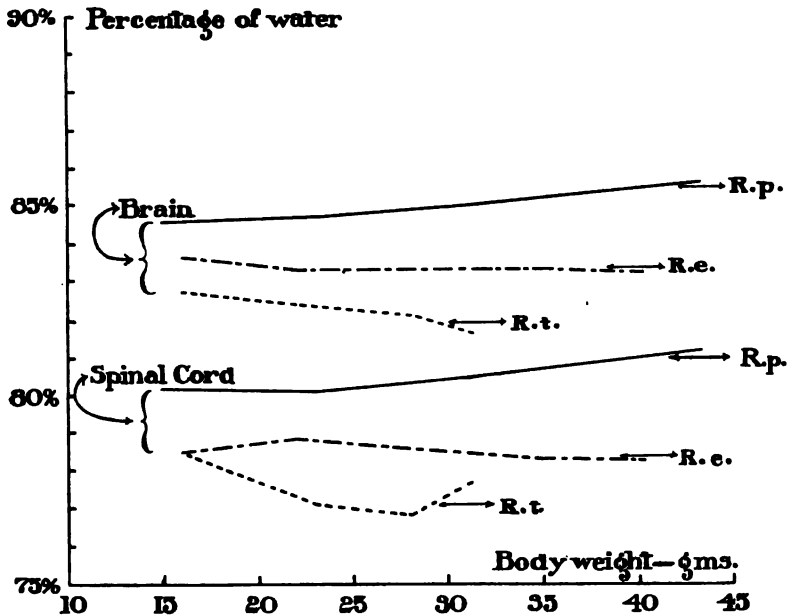


CHART 5.

Showing the percentage of water in the brain and in the spinal cord.

R. p. = *Rana pipiens*.
 R. e. = *Rana esculenta*.
 R. t. = *Rana temporaria*.

These differences in a character in which we might expect a high degree of similarity, call for some comment touching the trustworthiness of the results.

First, as to *R. pipiens*; the percentages in this species are the highest. The best evidence for their general correctness is furnished by the following table, extracted from the unpublished observations (1901) previously mentioned. At each date given

in Table 14 the percentage of water was determined in a group of eight frogs (4 males and 4 females) and seventeen such records are here reported. The body weight of the frogs in each group was the same, that is, 25 grams, approximately.

The range in the entire series here given is for the brain from 84.2 per cent to 86.2 per cent, and for the spinal cord from 78.8 per cent to 81.6 per cent, while the average of the four entries for the month of August, is for the brain 85.1 per cent and for the spinal cord 80.5 per cent. These are very close to the values for the second and third groups of *R. pipiens* (with a body weight near 25 grams) as given in Table 13.

TABLE 14.

Percentages of water in the brain and in the spinal cord of *R. pipiens*. Average body weight is 25 grams. Each entry is based on a determination for eight specimens (4 males and 4 females). From an unpublished study on the influence of season made in 1901.

DATE.	PERCENTAGE WATER IN	
	OF BRAIN.	CORD.
June 5.....	86.2	81.2
12.....	85.8	79.5
19.....	85.4	81.3
26.....	85.8	81.2
July 1.....	85.7	81.2
8.....	84.3	79.8
15.....	84.4	79.8
22.....	85.1	80.9
29.....	85.2	81.2
Aug. 5.....	84.6	79.6
12.....	85.2	80.6
19.....	85.1	81.6
26.....	85.3	80.0
Sept. 2.....	84.8	80.3
9.....	84.2	78.8
16.....	85.6	81.2
23.....	84.4	80.1

It seems probable from this comparison that we have obtained a generally correct value for the percentage of water in *R. pipiens*. In the case of *R. temporaria*, the specimens were dried at Liverpool, but not weighed until I reached Zurich. There they were further dried for 24 hours in the oven that was also used for drying the *R. esculenta* material, and then were weighed. They were found to give (see Table 13) the smallest percentages of water. This naturally raised the question as to whether they had been completely dried. The evidence that the drying was complete is only indirect. It is as follows:

The brains and spinal cords of *R. esculenta* dried and weighed at Zurich, were left in the original weighing bottles from the summer of 1904 to the spring of 1907, when, after careful redrying, they were weighed at the Wistar Institute in Philadelphia.

The last series of weighings made at Philadelphia, differed from those made in Zurich in 1904, by an average of plus 0.1 per cent. The fact that there was a trifling *gain*, is probably to be credited to the different balances used. But whatever the explanation of this gain may be, it seems to show that the drying in Zurich was complete, and thus to warrant the use of the values for *R. esculenta* and *R. temporaria* as entered in Table 13.

Assuming that in any given locality, the humidity of the atmosphere might be a factor influencing the amount of water in the body of a frog, I made an examination of the humidity records from July 1 to September 1, 1904, taken by the weather bureaus at Liverpool, Zurich and Chicago. For the data with which to do this, I am indebted to the officials of the U. S. Weather Bureau, whose courtesy I desire to acknowledge with thanks.

The matter is far too complex to permit us to make here more than the most general statements, but I feel justified in stating that the humidity conditions at Liverpool in July, 1904, and at Zurich and Chicago in August, 1904, were not unusual. Further, that broadly-speaking, the humidity is greatest at Liverpool, intermediate at Zurich, and least at Chicago. It is to be noted that the percentage of water in the several species follows the inverse order, being most in the Chicago specimens, where the humidity is lowest, and least at Liverpool, where it is greatest; a suggestive result which invites further inquiry.

Two more comments are however desirable before leaving this general topic.

From previous studies, we should expect that the percentage of water in the brain and in the spinal cord would diminish with increasing age, for the measure of which we here take the body weight.

This decrease is clear and regular for the brain of *R. esculenta* and *R. temporaria*, is indicated though less regular, in the case of the spinal cords of these two species, but in *R. pipiens* is regularly reversed in the case of the brain, and irregularly reversed in the case of the spinal cord. This makes it highly probable that some disturbing influence has modified the percentage of water in

the brain and cord of *R. pipiens*, so as to mask the effect of age (size), but it is to be added that the disturbance thus produced is relatively small, and not sufficient to affect the distinctive differences between *R. pipiens* and the species here compared with it.

If the average values for the percentage of water in the brain and spinal cord of the three species are calculated from Table 13 we obtain the following:

TABLE 15.

Average values for the percentage of water in the brain and spinal cord of all three species, together with the difference between that for the brain and for the spinal cord in each species, and the relative amount of water in the spinal cord, that in the brain being taken as a standard.

	PERCENTAGE OF WATER IN		DIFFER- ENCE.	PERCENTAGE VALUE OF CORD DETERMINATION.
	BRAIN.	SP. CORD		
<i>R. pipiens</i>	84.97	80.50	4.47	94.7%
<i>R. esculenta</i>	83.35	78.55	4.80	94.2%
<i>R. temporaria</i>	82.17	77.62	4.55	94.4%

It appears from this table that the absolute differences in the percentage values for the brain and cord are similar in the three species, and that the determinations for the brain being taken as the standards the relative values of the determinations for the spinal cord are about alike, ranging from 94.2 per cent *R. esculenta*, to 94.7 per cent *R. pipiens*. The similarity in these relations speaks for the correctness of the general results.

In this connection it is natural to enquire how the weight relations of the central nervous system or its parts, might be affected if the percentages of water in *R. esculenta* and *R. temporaria* were raised to that found in *R. pipiens*. Calculations have been made, and the results show that the superiority of the entire central nervous system and of the brain in *Rana pipiens* would be diminished only slightly. On the other hand, the weights of all the spinal cords would be brought together, and *R. temporaria* given the heaviest cord.

Moreover, in general, the weight values in the two European species would be brought closer to one another.

These alterations would however not essentially modify any of the differences on which we have had occasion to lay emphasis.

For the foregoing comparison of the central nervous system and its parts, together with the determination of the percentage of water, data on all three species have been available. But before commenting on the results just given, I wish to present some observations based on the comparison of two species only.

These additional observations are on the peripheral nervous system and relate first, to the number of medullated fibers in the spinal nerve roots; comparing *R. esculenta* with *R. pipiens* (there being no corresponding observations on *R. temporaria*). Second, to the length of the internodal segments; comparing *R. temporaria* with *R. pipiens* (there being no corresponding observations on *R. esculenta*).

The number of medullated nerve fibers in the spinal nerve roots of R. pipiens compared with the number in R. esculenta.—In a female *R. pipiens* weighing 48.2 grams, HARDESTY ('99) reported 14,582² medullated nerve fibers in both roots of the ten spinal nerves of one side. This was a much larger number than had been found by BIRGE ('82) in a specimen of *R. esculenta* of greater body weight. To reduce BIRGE's figures for the specimen of *R. esculenta*, weighing 63 grams, to those for a specimen weighing only 48.2 grams, we have proceeded as follows:

The smallest frog in BIRGE's series, with a body weight of 1.5 grams, in which he enumerated 2992 motor fibers in the ventral spinal roots of one side, was selected as one limit, and to this frog the same proportion of sensory fibers as was found in the 63 gram specimen, was allotted, a concession which probably makes the number of sensory fibers somewhat too large.

The number of fibers corresponding to each gram of body weight between 1.5 grams and 63 grams was then determined. By this method, it was found that when the number of fibers in the spinal nerves of the 63 gram frog was reduced to the number for a 48.2 gram frog, it amounted to 92.8 per cent of that found in the 63 gram frog, or 8925 fibers. Thus the difference between the two species is (14,582—8925) 5657 fibers, or put in another way, *R. esculenta* has only about 61 per cent as many medullated nerve fibers in the spinal nerve roots as has *R. pipiens*. On reducing the original observations of BIRGE for the number of fibers in the

² By a clerical error the number was printed on p. 78 (HARDESTY '99) as 14,783. It should be 14,582, and consequently I shall use the corrected number subsequently, even when referring to HARDESTY's paper.

several nerve roots to 92.8 per cent of their value, we obtained the following table.

TABLE 16.

Number of medullated nerve fibers in the dorsal and ventral roots of the spinal nerves of one side.

NUMBER OF NERVE.	R. PIPiens (HARDESTY) 48.2 GRAMS.		R. ESCULENTA (BIRGE) ORIGINAL WEIGHT 63 GRAMS REDUCED TO 48.2 GRAMS.	
	Dorsal.	Ventral.	Dorsal.	Ventral.
II.....	132	1045	115	727
III.....	2496	1478	1530	905
IV.....	329	379	245	446
V.....	371	163	179	98
VI.....	299	127	208	106
VII.....	350	251	171	148
VIII.....	1108	377	521	132
IX.....	2108	1295	1022	807
X.....	1171	721	921	409
XI.....	61	321	38	197
Totals	8425	6157	4950	3975
Sums.....	14582		8925	
Ratios	1.36-1		1.24-1	

When the data in Table 16 are thrown into the form of curves, we have the relations exhibited in Chart 6.

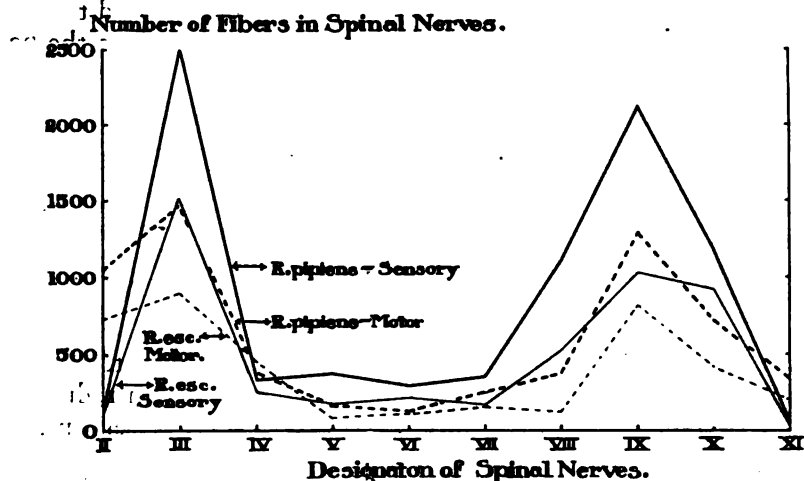


CHART 6.

Showing the numbers of medullated fibers in the spinal nerves of *Rana pipiens* and *Rana esculenta*.

From a study of Chart 6 we see that the form of the curves for the two species is very similar, even in details, although there are two evident differences.

In the first place, *R. pipiens* has regularly more fibers in each instance except in the ventral root of the IV spinal nerve, in which it has only 379 fibers against 446 in *R. esculenta*. In the second place, there is in *R. pipiens* a marked excess of fibers in the dorsal root of the IX nerve. In *R. esculenta*, the corresponding excess is distributed between the IX and X nerves. As a second specimen of *R. esculenta*, weighing 23 grams, examined by BIRGE ('82) shows a similar distribution, the possibility is suggested that this arrangement may be characteristic for *R. esculenta*.

The foregoing Table 16 also brings out the fact that the number of sensory, as compared with the number of motor fibers, is relatively greater in *R. pipiens*. Thus

	MOTOR.	SENSORY.
<i>R. pipiens</i>	1	1.36
<i>R. esculenta</i>	1	1.24

However a further analysis of this relation shows that in the lumbar nerves VIII, IX and X the proportions of motor to sensory are nearly alike in the two species.

	MOTOR.	SENSORY.
<i>R. pipiens</i>	1	1.833
<i>R. esculenta</i>	1	1.827

Moreover for the III nerve these proportions have been assumed as similar (see HARDESTY '99, p. 78), so that the difference which is found when the total number of fibers is compared, must depend on differences in this relation, which exists in the roots of the II, IV, V, VI, VII - - - XI nerves.

The ratio in this group of roots is

	MOTOR.	SENSORY.
<i>R. pipiens</i>	1	0.674
<i>R. esculenta</i>	1	0.555

Thus showing *R. pipiens* as superior in this last group, although in both species the ratio is less than unity.

As a consequence of these relations, it appears that while *R. pipiens* has everywhere a better sensory innervation, because there are absolutely more afferent fibers present for the same area

of skin and weight of muscle, the relative sensory supply is superior only in the head and trunk, but not in the skin and muscles of the limbs.

Such anatomical differences as these just described, suggest corresponding physiological differences between the two species. In pursuance of this suggestion, I sent out a letter of inquiry to my physiological colleagues in May of 1907. I take this opportunity of thanking my numerous correspondents for their courteous replies, but at the same time must report with regret that there do not appear to be any data bearing on the possible physiological differences, concerning which inquiry was made. The number of medullated nerve fibers in the spinal nerve roots of *R. temporaria*, has still to be determined.

A comparison of the length of the internodal segments in the fibers of the sciatic nerve of R. pipiens and R. esculenta.—As the heading indicates, the comparison will here be limited to fibers from one nerve. BOYCOTT ('04) has determined the length of the internodes in fibers taken from the sciatic nerve just at the point where it divides into the nervus tibialis and the nervus peroneus. The length of the internodes at this locality depends on two factors, first the size (length) of the frog, and second the diameter of the fiber; the internodes becoming longer, the larger the frog and the greater the diameter of the fiber examined.

By a study of specimens of *R. temporaria* of different lengths, BOYCOTT was able to show that the average length of the internodes of fibers of all diameters taken from the sciatic, increased in the same proportion as the length of the sciatic, the curves representing the two series of measurements running parallel. Accepting this result, it is possible to calculate the average length of the internodes at this point for frogs of different sizes.

Below is given a table containing the data on the six largest specimens of *R. temporaria* examined by BOYCOTT ('04, p. 375). These are arranged in the order of increasing body length, the measurement being made from the tip of the nose to the end of the urostyle.

The body weight here given was taken as usual. The length of the sciatic in millimeters is defined by BOYCOTT (*loc. cit.*, p. 371), as follows: "The upper end has been taken throughout as the point of emergence from the vertebræ of the upper of the two larger branches of the plexus.

There is no good fixed point for the lower end, the one which has been adopted as the cut end, obtained by cutting across the leg through the knee joint at right angles to the axis of the leg when it is in full extension."

TABLE 17.
R. temporaria.

No. of SPECIMEN.	BODY WEIGHT IN GRAMS.	LENGTH OF SCIATIC IN MM.
XXI.....	15.10	46.0
XXII.....	20.15	45.0
XXIII.....	16.45	45.5
XXIV.....	18.15	50.0
XXV.....	20.80	49.0
XXVI.....	24.80	53.5
Average	19.20	48.2

To compare with these, we have observations on four specimens of *R. pipiens*, made by Mr. TAKAHASHI³ in the Neurological Laboratory of the University of Chicago.

The specimens examined by TAKAHASHI, and in which the internodes were studied in the same locality as that selected by BOYCOTT, were four in number, and the measurements made on them are given in the following table:

TABLE 18.

No. of SPECIMEN.	BODY WEIGHT IN GRAMS.	SCIATIC LENGTH IN MM.* (CALCULATED.)
III.....	26	49.
V.....	34	53.3
VI.....	37	60.2
VIII.....	63	65.8
Average	40	57.3

* This measurement was not made by Mr. TAKAHASHI, but has been calculated from other data in his tables.

In accordance with BOYCOTT's results, we should expect in this series of *R. pipiens*, with an average sciatic length of 57.3 mm. to find longer internodes than in the series of *R. temporaria*, with an average sciatic length of only 48.2 mm., but on the contrary, the internodes in *R. pipiens* are much shorter. To make the comparison fair however it is necessary to reduce the measurements on *R. pipiens* to the measurements of the *R. temporaria* series,

³ Mr. TAKAHASHI kindly allows me to use the data from his forthcoming paper on the internodes in *R. pipiens*.

which is taken as the standard. To do this, we divide the observed values for the *R. pipiens* series by 1.188, since 57.3 mm., the average length of the sciatic in the series of *R. pipiens* is 118.8 per cent of 48.2 mm., the average length of the sciatic in the series of *R. temporaria*.

The observations thus reduced to the same standard are given in the following table.

TABLE 19.

Giving the lengths of the internodal segments in μ on the medullated fibers of the sciatic nerve, for frogs with a sciatic length of 48.2 mm., arranged according to the diameter of the fibers.

NUMBER OF OBSERVATION	R. TEMPORARIA (BOYCOTT) LENGTH OF INTERNODES	DIAMETER OF FIBERS.	R. PAPIENS (TAKAHASHI) LENGTH OF INTERNODES.	NUMBER OF OBSERVATIONS	RELATIVE VALUE OF LENGTHS IN R. PAPIENS.
In all about 1050	767	5-5.9 μ	500	159	65%
	*1186	6-6.9 μ	586	107	49%
	1102	7-7.9 μ	705	92	64%
	1159	8-8.9 μ	826	16	71%
	1288	9-9.9 μ	917	4	71%
	1399	10-10.9 μ	929	47	66%
	1416	11-11.9 μ	942	14	66%
	1536	12-12.9 μ	1027	5	66%

* As will be seen, Boycott's value for the length of the internodes in fibers 6-6.9 μ in diameter, is plainly aberrant, and therefore the percentage value for the internodes of fibers having this diameter in *R. pipiens*, is excluded from the general average.

The foregoing table shows that when grouped according to diameters, the internodal lengths in *R. pipiens* range between 64 per cent and 71 per cent of that in *R. temporaria*, the average being 67 per cent.

It follows from this that *R. pipiens* has three sheathing cells on a fiber, where *R. temporaria* has only two, and therefore more cells in the length of the sciatic.

Consequently *R. pipiens* has the finer and more complete construction, although it is not possible to say what physiological advantage goes with this difference in structure. There are no observations on *R. esculenta* to compare with those just given.

CONCLUSIONS. From the observations presented, we conclude that the three species studied are similar in general form and proportions, but that *R. pipiens* has:

1. A heavier central nervous system.

2. A heavier brain and spinal cord.
3. A heavier brain in proportion to the weight of the spinal cord.
4. A greater percentage of water in both the brain and spinal cord.
5. A larger number of both sensory and motor medullated fibers in the spinal nerves (when compared with *R. esculenta*).
6. A slightly greater proportion of sensory fibers in the spinal nerves (when compared with *R. esculenta*).
7. Shorter internodes, and therefore a greater number of sheathing cells (when compared with *R. temporaria*).

With the possible exception of the percentage of water, the interpretation of which is not yet clear, all these characters may be counted to the credit of *R. pipiens* as indicating a higher development of its nervous system, and if we may make these characters a basis for physiological predictions, we should expect the American leopard frog, *R. pipiens*, when compared with the European, *R. esculenta* and *R. temporaria*, to give (1) more perfect general reactions associated with (2) less perfect reflex ones, and also to be both (3) stronger and (4) more sensitive.

APPENDIX.

The observations of Fubini, '81.

In 1881 FUBINI published, under the title "Gewicht des Centralen Nervensystems im Vergleich zu dem Körpergewicht der Thiere bei *Rana esculenta* und *Rana temporaria*," a study of the weight of the brain and spinal cord in the two European species commonly used for experiment. His data are comprised in eight tables, each sex being represented by four tables, and the records on twelve specimens entered in each table. His main object in this study was to show that in the female frog, the weight of the central nervous system was less than in the male. As I have elsewhere explained (DONALDSON and SCHOEMAKER, '00), he does not show this, having fallen into error by reason of his failure to appreciate that the relative weight of the central nervous system diminishes with the increasing body weight of the frog.

Despite this failure in the interpretation of his records, it was desirable to examine further his original tables in order to deter-

mine what he had recorded concerning the weight of the brain and spinal cord.

The weight of the brain and of the entire central nervous system is given in all the tables. The weight of the spinal cord can be obtained therefore by subtracting the former from the latter. Having the weight of the brain and spinal cord, we can find the ratio between them.

There are moreover two tables, one for each species, in which we have the body weights of males to compare with the weight of the central nervous system. In the other six tables, the body weights for the males (two tables) are given "after evisceration" and for the females (four tables) without correction for ova. In these cases the body weights can only be estimated.

These data have been carefully worked over, with a view to determining how they compare with my own.

In the first instance, FUBINI's observations on the brain weights in unopened males of *R. temporaria*, are closely similar to mine. He obtains, however, weights for the spinal cord nearly double mine; thus his brain cord ratio is abnormally low. This is shown in the following table.

TABLE 20.

Showing the ratios of brain weight to the cord weight as determined by FUBINI, and by me.

Rana temporaria

DONALDSON REPETITION OF TABLE 12. BODY WEIGHT.	RATIO.	FUBINI BODY WEIGHT.	RATIO.
15.9	2.15	23.1 (male observed)	1.26
23.1	1.86	25.0 (male estimated)	1.70
28.0	1.87	31.0 (female estimated)	1.14
31.3	1.87	35.0 (female estimated)	1.77

Rana esculenta.

DONALDSON REPETITION OF TABLE 12. BODY WEIGHT.	RATIO.	FUBINI BODY WEIGHT.	RATIO.
15.9	2.29	20.0 (male estimated)	1.76
22.0	2.22	28.2 (male observed)	1.25
35.0	2.09	30.0 (female estimated)	1.80
40.2	2.05	35.0 (female estimated)	1.62

In the same way his observations on the weight of the brain in *R. esculenta* run only 10 to 15 per cent below mine, but the weights for the cords are much higher than mine, and the ratios as seen in the above table, are quite impossible and hopelessly irregular.

In view of these relations of brain to cord, I conclude that FUBINI's results are in general not trustworthy, and therefore do not require further discussion.

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PRELIMINARY NOTE ON THE SIZE AND CONDITION OF THE CENTRAL NERVOUS SYSTEM IN ALBINO RATS EXPERIMENTALLY STUNTED.

BY

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For these observations five litters of rats were so divided into two groups that the average body weight was nearly the same in both and one group was given the full laboratory ration, while to the other was fed the minimal amount of bread, corns and cereals.

The normally fed group constitutes the "first controls," and the underfed rats, the "stunted group." For further comparison, young rats with the approximately same body weight as the "stunted group," but much younger, were taken for the "second controls."

Beginning at the age of thirty days, the underfeeding considerably retarded the growth of the stunted group so that when they were, on the average, 170 days old they weighed 91.5 grams, whereas the "first controls"—of the same average age—weighed 146.5 grams. The younger rats from 80 to 100 days old which formed the "second controls," weighed on the average 86.3 grams. It must be remembered that during the time the behavior experiments were carried on (for nearly thirty days), the experimented rats were fed with normal diet and as a consequence these rats gained somewhat rapidly in body weight. Therefore the possibility of obtaining permanently stunted rats by means of underfeeding is still undetermined. All the rats were killed and weighed immediately after the behavior experiments were ended.

The main results obtained from the present experiments are exhibited in the following table.

External characters.—The most conspicuous external differences between normal and stunted rats as shown by the stunted rats are in the length of the body and of the tail, both of which

were considerably reduced with respect to the body weight.¹ This peculiar difference, as is seen from the table, holds true in every case. Further, the ratio between the length of the body and

TABLE I.

SEX.	AGE.	BODY WEIGHT.	BODY LENGTH.	TAIL LENGTH.	RATIO, BODY LENGTH TO TAIL LENGTH.	BRAIN WEIGHT OBSERVED.	BRAIN WEIGHT CALCULATED.	SPINAL CORD WEIGHT.	PERCENTAGE OF WATER, BRAIN.	PERCENTAGE OF WATER, SPINAL CORD.	REMARKS.
	<i>days.</i>	<i>grams.</i>	<i>mm.</i>	<i>mm.</i>							
F.....	215	186.2	189	158		1.8996		.5597	78.365	70.573	1st control
F.....	215	106.2	155	112		1.6325		.4030	78.623	72.641	stunted
F.....	80-100	105.7	155	131		1.6313		.4049	78.900	72.925	2d control
M.....	182	186.7	190	154		1.6578		.4862	78.447	70.547	1st control
M.....	182	113.7	155	109		1.5678		.3756	78.772	73.003	stunted
M.....	80-100	99.7	157	121		1.7029		.4059	78.971	73.121	2d control
M.....	164	119.1	167	130		1.6671		.4524	78.315	71.353	1st control
M.....	164	77.6	137	100		1.5884		.3573	78.374	71.760	stunted
M.....	80-100	87.4	154	119		1.7156		.3579	78.870	72.981	2d control
F.....	164	126.9	170	139		1.6859		.4941	78.118	71.623	1st control
F.....	164	89.3	140	113		1.6053		.3730	78.477	72.193	stunted
F.....	80-100	61.7	128	113		1.4880		.2975	78.568	71.092	2d control
F.....	127	113.2	160	135		1.7698		.4459	78.675	72.303	1st control
F.....	127	70.9	132	105		1.7394		.3404	78.836	73.413	stunted
F.....	80-100	77.2	139	115		1.5110		.3359	79.139	73.861	2d control

Averages.

F + M	170	146.4	175	143	1 : 0.823	1.7360	1.772	.4877	78.384	71.280	1st control
F + M	170	91.5	144	108	1 : 0.750	1.6267	1.646	.3699	78.616	72.602	stunted
F + M	80-100	86.3	147	120	1 : 0.816	1.6098	1.629	.3604	78.889	72.796	2d control

* This is the only exceptional case, where percentage of water in the second control is less than that of the stunted.

that of the tail is considerably less in the stunted rats than in the control rats. The ratio just mentioned is found to be on the average 1 : 0.82 in both "first" and "second controls" while

¹ The measurement taken from the tip of the nose to the anus is designated as "body length" while that from the anus to the tip of the tail is designated "tail length."

in the stunted rats the ratio is 1 : 0.75. Underfeeding therefore produces short tailed individuals. The nature of this result has still to be investigated.

Central nervous system.—The weight of the brain and spinal cord and the percentage of water in both were separately determined according to the usual procedure.

The weight of the encephalon was found to be normal to the body weight in both the controls and stunted rats, the brain weight of the first controls is heaviest and that of the "stunted" and "second controls" follow in the order named. The relation between body and brain weights was tested by the formula,

$$\text{Brain weight} = 0.554 + 0.569 \log (\text{body weight} - 8.7).$$

This formula has been developed through the study of our laboratory records and gives us the theoretical weight of the brain for any body weight. The former was found to be normal even in the stunted group. As seen from the table, the difference between calculated and observed brain weights on the average was about 1.5 per cent, indicating a normal relation of the brain weight to the given body weight. Thus we conclude that the normal relation between the body and brain weights was not disturbed by stunting.

We have as yet no satisfactory method for determining the normal weight of the spinal cord in respect to either body weight or any other characters. Nevertheless the proportional weight of the spinal cord in the experimented and in the second control rats with respect to the brain and body weights suggests that it also has grown normally (see Table I). Therefore we conclude that the weight of the spinal cord and brain are similarly related to the body weight. Consequently so far as the weight of the central nervous system is concerned, the normal relation to the body weight is still maintained by the stunted rats.

It is interesting to note in this connection that the definite relation between the body and brain weights is not disturbed even when the growth of the body has been considerably accelerated by means of the lecithin² or when the rats have been once starved and then returned to normal diet so that the final body weights

² The effect of lecithin on the growth of the white rat. *American Journal of Physiology*, vol. 10, no. 1. 1905.

become normal to the given age.³ Whether or not this definite relation between the brain and body weights can still be maintained even when we modify the conditions in other ways will be the subject of further investigations.

Percentage of water in the central nervous system.—The percentage of water in the central nervous system was always higher in the stunted rats than in the first controls, despite the fact that ages of the two groups were the same. On the other hand, this value in the stunted rats—though slightly less—was very close to that of the second controls which were much younger. It has been established in the laboratory that among rats of the same age, those with heavier brains have a smaller percentage of water than those with lighter brains. Therefore the higher percentage of water in the stunted rats as compared with the first controls indicates “a usual” rather than “an unusual” condition, since we should expect to find a somewhat higher percentage of water in the rats with less heavy brain at a given age. We conclude therefore that the percentage of water in the central nervous system in both the controls and stunted rats is normal, in the latter of course having due regard for age and body weight, as well as weights of the brain and spinal cord.

Since the percentage of water and that of the extract are inversely related we may infer that somewhat greater percentage of water found in the central nervous system in the stunted rat indicates with highest probability relatively smaller development of the medullated nerve fibers in that organ when compared with that of the first controls. This statement is correct at least for the peripheral system, as a recent investigation⁴ by Mrs. J. W. HAYES shows that the number of medullated fibers in the second spinal nerve in heavier albino rats is greater than that in the less heavy rats of the same age. A further discussion of this general point is however reserved for a future publication.

Conclusions.—Our final conclusions are, then, that aside from the shorter length in the body and tail, which is not only absolute but relative also, the stunted rats differ from the normal rats only in the absolute magnitude of the measured characters, while, on the other hand, when differences in the central nervous system

³ Effect of partial starvation followed by a return to normal diet on the growth of the body and central nervous system of albino rats. *American Journal of Physiology*, vol. 17, no. 5. 1907.

⁴ As yet unpublished.

are compared with the growth of the entire body the growth of the stunted rats may be considered just as normal as that of the controls.

The stunted rats were made the subject of tests, by Mr. JOHN W. HAYES, fellow of psychology in the University of Chicago, to determine whether their behavior was modified by their arrested growth, and the results will be published by him later.

ON THE PHYLOGENETIC DIFFERENTIATION OF THE ORGANS OF SMELL AND TASTE.

BY

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There are in vertebrates two systems of sense organs adapted to respond directly to peripheral chemical excitation, the organs of smell and taste. In this respect they are in contrast with the other sense organs of the body; but when we come to compare the two chemical senses with one another we find it difficult to discover any objective difference between their stimuli or any explanation for the development of two chemical senses in the primitive aquatic vertebrates. And yet the very lowest vertebrates exhibit important morphological differences between the peripheral organs of smell and taste, a complete separateness in the nervous pathways to the brain and still more important differences in the central reflex connections within the brain. In view of the similarity in the nature of the stimuli to which the peripheral organs respond, these fundamental central differences have thus far baffled explanation.

Let us first consider briefly the criteria by which in the case of human beings the modalities of sense may be distinguished. (1) Doubtless the most important criterion for us is direct introspective experience, the *psychological* criterion. (2) The adequate stimuli of the various senses exhibit characteristic physical or chemical differences, the *physical* criterion. (3) The data of anatomy and physiology may differentiate structurally the receptive organs and conduction paths of the several types of sensation, the *anatomical* criterion. (4) The type of response varies in a characteristic way for the different senses, the *physiological* criterion.

It is impossible in the present state of our knowledge to frame adequate definitions of all of the senses in terms of any one of these criteria alone. Thus, we are not able introspectively to dis-

criminate between olfactory and gustatory sensations, but rather elaborate physiological experimentation is necessary to enable us to effect the analysis of these two sets of stimuli. Again, the anatomical and physiological bases of several of the senses are still very imperfectly known and in still other cases we are almost wholly ignorant of the distinctive chemico-physical qualities of the stimuli which call forth diverse sense modalities. The latter point is notably true for the senses of smell and taste. The common statement that we smell substances only in the gaseous state and taste liquids (solutions) is only approximately true, if at all, in the mammals, and certainly cannot hold for the lowly aquatic vertebrates where the differentiation of these two sense organs in practically their definitive form first occurred.

Attention has been drawn to the fact that, while tastes can be classified under the four subjective qualities, sweet, sour, bitter and salty, the innumerable odors are apparently quite incapable of any such classification. To this it may be added, on the one hand, that ZWAARDEMAKER claims to be able to classify the known odors into some nine groups which he compares with the four classes of taste, and, on the other hand, that some recent studies on the chemical physiology of taste¹ go to show that it is a reaction between the receiving organ and the ions of the sapid substances and that the ions belonging to a given group, such as those giving "salty" tastes, do not all produce the same sensation quality. In other words, the four groups of taste qualities, like the nine groups of smell qualities, are more or less ill defined both from the standpoints of their psychological and their physico-chemical criteria. It is to be expected that future research will shed additional light on the physical and psychological criteria of smell and taste, but it will not eliminate their strong similarity.

These considerations suggest that smell and taste have originated phylogenetically from a common undifferentiated chemical sense, a conclusion which is supported by the morphological relations of their cerebral centers. The details of this anatomical evidence are far too complex to be summarized here and the reader

¹ L. KAHLBERG: The action of solutions on the sense of taste. *Bul. Univ. Wisconsin, Science Series*, vol. 2, pp. 1-31. 1898.

T. W. RICHARDS: The relation of the taste of acids to their degree of dissociation. *Am. Chemical Journal*. 1898.

is referred to the exposition and discussion of the cerebral centers for smell and taste given by JOHNSTON and HERRICK.²

But despite these fundamental similarities, it still remains true that the organs of smell and taste are topographically widely separated and structurally very different both peripherally and centrally. Their central neural pathways and connections are in fact as different as are those for hearing and vision, two senses whose psychological and physical criteria are most clearly defined. The anatomical relations of the gustatory system are known in lower vertebrates and those of the olfactory system are well understood and are tolerably uniform throughout the vertebrate series. It is possible to determine by experiment to which one of the peripheral sense organs an animal responds when given a chemical stimulus. The anatomical criteria of smell and taste are therefore clearly defined.

As far as vertebrates are concerned, we may define taste in accordance with the anatomical criterion as the reaction or sensation arising from the appropriate chemical stimulation of the organs known as taste buds (wherever found in the body), and smell as the reaction or sensation arising from the appropriate chemical stimulation of the termini of the olfactory nerve. (See the Addendum, p. 165.)

These definitions cannot be extended to the invertebrates unless homologous organs can be discovered among them. It may well be that there are no such organs in the invertebrates, a single chemical sense alone serving their needs; or two or more chemical senses may be present among the invertebrates which are wholly unlike either of the vertebrate senses.

In this discussion it will be observed that I take a somewhat different standpoint from that of NAGEL,³ who defined taste and smell in terms of the state of physical aggregation of the stimulus. Smell, he says, is the faculty of perceiving vaporous (*dampförmige*) substances and taste is the faculty of perceiving liquid substances. It follows from this, he argues, that it is not proper to attribute to aquatic animals a sense of smell in addition to a sense of taste, but both functions fuse into a single one.

² J. B. JOHNSTON: The nervous system of vertebrates. Philadelphia, 1906, chap. 10.

C. JUDSON HERRICK: The central gustatory paths in the brains of bony fishes. *Journ. Comp. Neurol. and Psych.*, vol. 15, 1905, pp. 450-454.

³ W. A. NAGEL: Vergleichend physiologische und anatomische Untersuchungen über den Geruchs- und Geschmackssinn und ihre Organe, mit einleitenden Betrachtungen aus der allgemeinen vergleichenden Sinnesphysiologie. *Bibliotheca Zoologica, Stuttgart*, Heft 18. 1894.

His argument for the absence of smell in all aquatic animals is based upon the definition of smell as the perception of gaseous or vaporous stimuli. He adduces evidence that when air is dissolved in water it is incapable of absorbing the vapors given off by volatile substances unless these vapors are soluble in the water itself, stating that they cannot be dissolved in the air contained in the water. They affect the organs, therefore, as true solutions, not as gases dissolved in water. He says (p. 60), "All substances which pass over into water from an object lying in the water, say a decomposing organic body, diffuse themselves in the water in accordance with the laws of the diffusion of liquids, not those of gases and vapors, even though the object in question when brought into the air may have vaporous emanations."

It is unnecessary to summarize here his elaborate argument for the absence of smell in fishes based upon anatomical differences in the receptive olfactory organs between fishes and air breathing vertebrates; for when examined closely in the light of our present knowledge these differences are seen to be trifling when compared with the broad resemblances of both peripheral and central organs of smell throughout the whole vertebrate phylum.

NAGEL's conclusion is expressed on p. 62: "We can with the greatest probability assume that the end-buds of the glossopharyngeus in the mouth of fishes and amphibians serve the chemical sense, viz: taste, and thus function in eating. We can with some probability assume that the sense organs of fishes and aquatic amphibia supplied by the N. olfactorius likewise serve the chemical sense; but this is certainly no olfactory organ in the sense of that term in the land animals. What the occasion of its chemical excitation may be is quite unknown. The method by which it is excited is with highest probability similar to the excitation of the taste buds in the mouth, i. e., the excitation follows through substances dissolved in water."

This conclusion, to my mind, simply illustrates the fact that it is impossible in the present state of our knowledge to interpret these two senses in terms of the physical stimuli. It is not meant to imply that there is no difference between the physical stimuli of smell and taste; for I think it probable that further research will bring such differences to light. But these differences are apparently very small in aquatic animals, whereas the structural differences between the nervous apparatus involved are very great indeed, even in the lowest fishes.

Our argument thus far leads to an apparent *impasse*. The physical and psychological criteria of smell and taste seem inadequate to account for the definite and fundamentally different anatomical peculiarities of the organs in question. But we have not yet considered the fourth line of evidence mentioned at the beginning, that which we called the physiological criterion; viz: the characteristic responses normally following the stimulation of these organs of sense.

A suggestion made by Professor SHERRINGTON in his recent Lectures on the Integrative Function of the Nervous System seems to me to put the matter in a perfectly clear light. As is well known, SHERRINGTON classifies the sense organs (receptors) into (1) exteroceptors, adapted for response to stimuli arising from without the body; (2) proprioceptors, sense organs lying within the body adapted to report to the central nervous system the physiological state of the organs of somatic response themselves (typified by muscle spindles, neuro-tendon organs, etc.); (3) interoceptors, organs set to guard the receptive surfaces of the body—enteron, lungs, etc. Exteroceptors which are excited by stimuli arising at a distance from the body are termed by SHERRINGTON distance receptors.

The physiological analysis here outlined is full of helpful suggestion in the morphology of the nervous system. Putting SHERRINGTON's analysis into correlation with that of the new school of functional morphologists, we recognize his first two types of receptors as falling within the somatic sensory group, for the chief organs of response (effectors) in both cases are the somatic or skeletal muscles. SHERRINGTON's third type is the visceral sensory system, calling forth reflexes in the visceral musculature (including the specialized striated visceral muscles of the branchial arches and their derivatives in the higher vertebrates).

The taste buds lying within the mouth of vertebrates are typical interoceptors, and they with their nerves and cerebral centers are classified as specialized visceral sensory organs. They are in gnathostome vertebrates usually stimulated by food contained within the mouth and the effectors with which they are most directly connected are the visceral muscles of the jaws, gills, œsophagus, etc. In the protochordate vertebrate ancestry it is probable that there was but one chemical sense, and that feebly developed; for these animals probably did not masticate their

food, and the undifferentiated primordial chemical sense may have been as important in determining the chemical character of the environing water as of the food eaten.

Be that as it may, with the appearance of teeth which pierce or crush the food, the organs of chemical sense within the mouth and pharynx assumed an important function as guardians of the entrance to the œsophagus, an interoceptive function which they perform in all gnathostome vertebrates—the organs of taste. Parallel with this differentiation within the mouth, the organs of chemical sense lying outside the mouth at the rostral end of the body would assume more and more importance as organs for detection of chemical differences in the surrounding water, differences resulting usually from the presence of sources of chemical alterations of the water lying outside the body of the fish. These external organs of chemical sensation in the leading segments of the body were finally aggregated as the organ of smell.

The differences in the character of the stimulus applied to these two organs may have been very slight at the beginning (and indeed may be so still); but in the case of any organism possessing the power of free locomotory movement the physiological significance of the stimulation of the two sense organs may be very different indeed. The object which acts as a stimulus to taste buds is already within the mouth. The appropriate reaction is typically a contraction of the visceral musculature of the mouth and pharynx adapted either to masticate and swallow or to eject the object, as the case may require. The somatic musculature is not necessarily brought into play. The olfactory organ, on the other hand, has become a distance receptor and the appropriate reaction is a movement, usually locomotor in type, of the somatic muscles, taking the animal toward or away from the source of the stimulus. Even though the stimuli in the two cases were identical, it is evident that the difference in the character of the response would bring into play a very different central reflex apparatus for the distance reaction from that for the mastication or swallowing reflex.

This difference between the characteristic reaction of the interoceptor and the distance receptor is in my opinion the sufficient explanation for the most important structural differences between the olfactory and gustatory systems of vertebrates. This same feature involves, it is true, a certain degree of difference between

the physical stimuli and the psychical qualities of odors and savors, especially in the higher vertebrates; but these are in all animals quite subordinate to the type of reaction involved.

A critical examination of the central conduction paths for smell and taste supports this view of the case. The central olfactory apparatus is very constant throughout the vertebrate phylum. The organ of smell, as befits a distance receptor, is located in the leading segments and its central connections are with the extreme tip of the neural tube; indeed in all of the true vertebrates it has grown out rostrad beyond the primary neural tube, the entire rhinencephalon lying in the telencephalon, or ultra-terminal brain. The path extends from the olfactory bulb to the tuberculum olfactorium and other structures in the base of the forebrain, thence directly back to the olfactory centers in the thalamus or else first to the olfactory cerebral cortex (hippocampal formation, etc.) and then to the thalamus. The two principal olfactory centers in the thalamus lie in the epithalamus and hypothalamus respectively. Each of these thalamic centers receives in higher vertebrates olfactory tracts from both the basal and cortical olfactory centers of the forebrain; and each sends a strong tract to reach the motor centers. These tracts are the tr. habenulo-peduncularis (fasc. retroflexus or bundle of MEYNERT) and the fasciculus pedunculo-mammillaris (tr. mamillo-bulbaris). In lower vertebrates both of these tracts can be traced far downward into the medulla oblongata, where they come into relation directly with the motor nuclei of the cranial nerves and the evidence is that either directly or indirectly they pass still farther into the spinal cord for the somatic motor reflexes characteristic of olfactory reactions.

The central gustatory path is well known only in fishes. Here there are much more direct reflex connections with the visceral motor nuclei of the cranial nerves than the olfactory system shows, and in most fishes no important connections with somatic motor nuclei save by way of the hypothalamus and tractus mamillo-bulbaris. There are certain fishes, however, in which taste buds have been developed secondarily in the outer skin of the general body surface. Here they have been shown to function as exteroceptors⁴ and in these cases the central connections of the cutaneous taste

⁴C. JUDSON HERRICK: The organ and sense of taste in fishes. *Bul. U. S. Fish Commission for 1902. Washington, 1904.* The central gustatory path in the brains of bony fishes. *Journ. Comp. Neurol. and Psych.*, vol. 15, no. 5. 1905.

buds are very different from those of the phylogenetically older taste buds within the mouth. In the catfish and carp the primary cerebral center for all of the cutaneous taste buds is the facial lobe, from which secondary gustatory tracts of the typical sort pass out to the visceral motor centers, and in addition a direct secondary path to the funicular nuclei where these gustatory impulses are coördinated with tactile impressions from the same areas of skin.⁵ A single path leaves the funicular nuclei for the somatic motor centers, thus serving as a common reflex path for both tactile and gustatory impulses from the skin. In the cod⁶ the cutaneous taste buds effect somatic motor connections in an entirely different way, passing directly from the equivalent of the facial lobe into the fasciculus longitudinalis medialis and thence to the somatic motor nuclei, indicating that the cenogenetic connection of the taste buds which act as exteroceptors with somatic motor centers has been acquired independently in the gaidoids and the Ostariophysi.

The interesting point in this connection is that within the group of teleosts taste buds, which typically in fishes act as interoceptors, have secondarily acquired exteroceptive functions, and parallel with this change a new central reflex path has been established between the primary centers of cutaneous (exteroceptive) taste and the somatic motor centers. It is probable that at a much more ancient period in the phylogeny of vertebrates an analogous differentiation took place in the primordial unspecialized chemical sensory apparatus, one part becoming a typical interoceptor (gustatory apparatus) and establishing its most direct central reflex connections with the visceral muscles of mastication, deglutition, etc., and another part becoming a typical exteroceptor (olfactory apparatus) and early establishing direct central reflex connections with somatic muscles of locomotion, eye movements, etc., in addition to the visceral motor reflexes characteristic of a visceral system.

It should be expressly stated that the claim is not made that all anatomical differences between the organs of smell and taste are explained by this principle, but only that in this way the direction

⁵ C. JUDSON HERRICK: On the centers for taste and touch in the medulla oblongata of fishes. *Journ. Comp. Neurol. and Psychol.*, vol. 16, no. 6. 1906.

⁶ C. JUDSON HERRICK: A study of the vagal lobes and funicular nuclei of the brain of the codfish. *Journ. Comp. Neurol. and Psych.*, vol. 17, no. 1. 1907.

of the original phylogenetic differentiation was determined and that this is still the dominant feature of the two systems in question.

The conclusion is that the agencies which acted to produce the differentiation from each other of the senses of smell and taste are not to be sought primarily in the stimuli calling forth the reflexes, but rather in the character of the response evoked by the stimulus.

ADDENDUM. As these pages pass through the press an abstract of the very interesting experiments of PARKER appears in the Proceedings of the American Society of Zoölogists (*Science*, n. s., vol. 27, no. 690, March 20, 1908, p. 453). PARKER has previously determined that the skin of the body of the frog and of various other aquatic animals is sensitive to chemical stimuli. Quite in accord with those results, he now finds that the same is true for the common fresh water catfish, *Ameiurus*. This fish possesses taste buds innervated by the nervus facialis scattered in the skin over practically the whole body surface. If the nerves supplying these taste buds on the trunk are cut, the fish no longer reacts to a bait in the normal way (by turning to snap at the bait) when it is presented to the flank of the body. Nevertheless such operated fishes are sensitive to sour, saline and alkaline solutions when applied to the skin of the trunk.

These results, together with the control experiments described, demonstrate that the spinal nerves of this teleost, like those of the frog, are sensitive to certain external chemical stimuli. The important question at once arises, are these responses to chemical stimulation of the spinal nerves transmitted by the same nerve fibers which transmit the tactile stimuli, or by some other component of the spinal nerves? We know from abundant physiological and clinical experience that the cutaneous rami of the spinal nerves of man transmit impulses which are perceived introspectively as very diverse sensation qualities (touch, temperature, etc.). There is evidence that some at least of the different functions of the sensory spinal nerves are served by anatomically different neurone systems; but whether the ability to respond to direct peripheral chemical stimulation is limited to one or more of these systems or common to all of them, further experiment alone can determine.

Chemical irritability may prove to be more far-reaching and fundamental in nervous excitation than is commonly recognized. However this may be, two special reflex mechanisms have been very elaborately differentiated in vertebrates along quite diverse lines for precise and rapid response to special external chemical stimuli, the organs of smell and taste; and the explanation offered in the preceding pages for the phylogenetic differentiation of these two functional systems is not directly dependent upon any theory regarding the ultimate nature of the primordial undifferentiated sensory type from which they have sprung.

Professor PARKER concludes the note to which we have referred with the remark, "From these experiments it is to be concluded that the sense of taste in horn-pouts is complex and involves not only the seventh nerve, but also the spinal nerves." Assent to this proposition will be readily granted only if we define the sense of taste in accordance with the "physical criterion" (see p. 157) as NAGEL does. In the opinion of the writer neither this criterion nor the "anatomical criterion" (as I have used it on p. 159) alone is adequate *in the present state of our knowledge* to serve as the basis for generally acceptable definitions of all of the so-called senses. Pending the extension of our knowledge in these fields, fruitless controversy may be avoided by a clear recognition of the fact that harmonious conclusions can be expected only on the basis of an explicit understanding regarding the standpoint chosen in every discussion.

SOME CONDITIONS WHICH DETERMINE THE
LENGTH OF THE INTERNODES FOUND ON THE
NERVE FIBERS OF THE LEOPARD FROG, *RANA*
PIPIENS.

BY

KATASHI TAKAHASHI, *Rigakushi*.

(*From the Neurological Laboratory of the University of Chicago.*)

WITH SEVEN FIGURES.

INTRODUCTION.

In the winter of 1903-04, the following study of the growth of the internodes on the nerve fibers of the leopard frog, was begun, in order to determine whether on a lengthening nerve fiber the number of internodes increased or remained constant. While this study was in progress, the interesting paper by BOYCOTT '04, "On the number of nodes of Ranvier in different stages of the growth of nerve fibers in the frog," was published. The species of frog used by BOYCOTT was the common *Rana temporaria* (*fusca*) of England.

After briefly referring to the scanty literature on the subject of the internodes (see KÖLLIKER '96), which shows that they have different lengths in different species of animals, are longer in old than in young animals, and longer in fibers of great than in fibers of small diameter, BOYCOTT presents evidence which demonstrates beyond reasonable doubt, that in the growing sciatic nerve, at the point where it divides into the *nervus tibialis* and *nervus peroneus*, the *average length* of the internodes increases very nearly as does the length of the nerve itself. It would seem from this to follow that the number of internodes should remain constant. The calculations show however a very slight but regular increase in the estimated number of the internodes as the frogs become larger. This result, noted but not explained by BOYCOTT, and touched on later in this paper is, I believe, susceptible of an explanation, which at the same time leaves BOYCOTT's main conclusion intact.

The second important point brought out by BOYCOTT, although not especially commented on by him, is illustrated in the accompanying Table I, which is copied from BOYCOTT's paper, with a slight change made by putting the "sciatic length" in the column where the body lengths are given by him.

TABLE I.

Average internodal lengths (μ) corresponding to each diameter. *Rana temporaria* (fusca). Copied from BOYCOTT, *Journal of Physiology* (FOSTER), vol. 30, p. 373, 1904.

Diameter.....		2 μ	3 μ	4 μ	5 μ	6 μ	7 μ	8 μ	9 μ	10 μ	11 μ	12 μ	13 μ	14 μ	15 μ
GROUP.	SCIATIC LENGTH.														
	mm.														
I	18.2	205	339	450	524	535	631	657	660	667	797				
II	25.1		428	525	592	659	701	772	742	789	846	865	890		
III	34.5					770	819	770	878	968	1007	1069	1043	1177	
IV	46.6		570	1000	766	1186	1102	1106	1243	1358	1361	1490	1511	1576	1766

It is here seen that on fibers of a given diameter from small (young) frogs, the internodes are shorter than on fibers of the same diameter, taken from large (old) frogs, the size being indicated by the sciatic length. If we apply the notion of growth to the interpretation of this table, and remember that a fiber of a given diameter in the small frog, becomes a fiber of greater diameter in the large frog, then it is found that the average of the measurements in Group I of fibers from 2 μ to 11 μ in diameter, which is 546 μ , compared with the average of the measurements for fibers from 6 μ to 15 μ in diameter, in Group IV, which is 1370 μ , gives an increase in the length of the internodes amounting to 2.51, and this corresponds very nearly to the increase in the length of the sciatic nerve, from 18.2 to 46.6 mm., which is 2.56. As will be observed, the average difference in diameter in the two series compared is 4 μ .

This method of comparison is admittedly crude, but under the conditions, furnishes a satisfactory confirmation of BOYCOTT's general conclusion that the number of internodes is not increased during growth, but that their average length increases as does that of the nerve in which they are found.

In view of the results obtained by BOYCOTT, it was thought best in the present study to examine especially some points which he has left untouched.

These will be presented under the following heads:

1. The average length of the internodes at different levels along the nerves to the leg.
2. The length of the internodes at different levels on fibers of like diameter.
3. The length of the internodes on fibers in the roots of the spinal nerves.
4. The number of medullated fibers at different levels in the legs of tadpoles of increasing size.
5. A comparison of the length of the internodes in the American frog, *Rana pipiens*, with their length in the English frog, *Rana temporaria* (*fusca*).

Before proceeding to the discussion of the special topics, I desire to state that this study was made under the direction of Prof. H. H. DONALDSON, to whom I am indebted also for the revision of my manuscript. Moreover, I wish to thank both Dr. E. H. DUNN and Dr. S. HATAI for their aid and suggestions given to me during the conduct of this investigation.

MATERIAL AND TECHNIQUE.

For this study, the common leopard frog, *Rana pipiens* (SCHREBER) was used, the specimens having been obtained from a local dealer and probably collected in the country about Chicago. The frogs were killed with chloroform; the body weight, corrected for ova in the case of the females, was taken in a closed box, and the total length, i. e., the length from the tip of the nose to the tip of the longest toe, as well as the body length, i. e., from the tip of the nose to the tip of the urostyle, were both recorded. In some cases also, the length of both the dorsal and ventral roots of the III and IX nerves (GAUPP's numbering) was determined. The data thus collected are given in Table 2.

In preparing the material, the following methods were employed: A short piece of the fresh nerve was cut out and laid on a wedge-shaped strip of cardboard, the piece of nerve being extended to its normal length. This was fixed, and at the same time macerated, by being placed for twenty-four hours in the following solution (A):

Osmic acid.....1.00 per cent, 5 parts
 Chromic acid.....0.25 per cent, 3 parts
 Hydrochloric acid.....0.10 per cent, 2 parts

After washing for twenty-four hours in running water, the specimen was transferred for twenty-four hours to the following solution (B):

Glycerine10 parts
 50 per cent alcohol.....20 parts
 Hydrochloric acid0.09 parts

After this treatment, the specimens are preserved in solution (C):

Glycerine10 parts
 50 per cent alcohol.....20 parts

This last solution (C) should be renewed once or twice at intervals of twenty-four hours. Thick nerves were slit longitudinally with a razor, after they had been in solution (A) for two or three hours. This was done to assist the penetration of the fluid. The specimens were teased in solution (C).

TABLE 2.

Data on the specimens of *Rana pipiens* used in this investigation. Entries arranged in the order of increasing body length. V, ventral; D, dorsal.

No.	SEX.	BODY WEIGHT	TOTAL LENGTH.	LENGTH OF BODY.	LENGTH OF III SPINAL ROOTS.	LENGTH OF IX SPINAL ROOTS.	DATE OF KILLING.
		<i>grms.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	<i>mm.</i>	
1	M.	5.5	104	39	V .85 D .64	2.6 2.1	Aug. 29, '05
2	M.	23.5	169	71	V 2.6 D 2.5	7.0 6.5	Jan. '04 Jan. 29, '06
3	F.	26.0	166	72			
4	F.	27.2	180	78	V 2.4 D 2.4	7.7 7.1	Mar. '04 Dec. '03 Nov. '03
5	M.	31.0	192	80			
6	M.	37.0	204	80			
7	M.	61.1	226	89		V 9.5 D 9.0	July 16, '04
8	M.	63.0	222	89.4	V 2.0 D 1.6	5.9 5.4	Aug. 3, '05

The technique just given, fails however to yield satisfactory results when applied to the nerve roots of the III or IX nerve as the fibers become brittle and distorted. Moreover, the roots

of the III nerve do not yield to the technique which proved fairly satisfactory in the case of the roots of the IX nerve, so that the technical problem is complicated. In the case of the IX nerve, I used in the first instance solution (D):

Osmic acid.....	0.10 per cent, 4 parts
Chromic acid.....	0.02 per cent, 1 part

The specimen was left in this solution for twenty-four hours, then washed in running water for twenty-four hours, and finally preserved and teased in solution (E).

50 per cent glycerine.

This should be renewed several times.

Later, in place of solution (D), I used solution (F):

Osmic acid.....	0.100 per cent, 5 parts
Chromic acid.....	0.025 per cent, 1 part
Acetic acid.....	0.100 per cent, 1 part

This gave somewhat better results than solution (D) but none of these solutions acted upon the roots of the III nerve sufficiently well to justify an extended study of its fibers, hence only one III nerve was examined.

It is fundamental to the following argument, that the treatment of the nerves should not materially alter the length or the diameter of the fibers which are to be measured. It was necessary therefore to examine the effect of the solutions here employed, and this was done by measuring samples of the nerve as they were passing through the solutions.

Sixteen samples from different levels along the nerves to the leg were first measured, after having been for two or three hours in solution (A) and then finally measured after treatment in solution (C) when they were ready to be teased. The measurement showed an average loss in length of 3.6 per cent and an average loss in diameter of 12.8 per cent.

In the case of eight other specimens (four from the III nerve, and four from the IX nerve) examined in the same way, the loss in length was 1 per cent, and in diameter, 8.6 per cent.

The loss in length is trifling; that in diameter however seems large. It is probable nevertheless that it is to be mainly credited rather to a diminution in the connective tissue sheath, and to the

compacting of the fibers, than to a diminution in their individual diameters, and it is therefore not thought that the normal diameters of the fibers are as much modified as the above measurements would indicate.

The samples of nerve were teased with fine needles under a dissecting microscope, and measured directly with a compound microscope, using lenses and eyepieces (with micrometer scales), suited to the determination of length on the one hand and diameter on the other.

The full series of individual measurements will not be printed here, but the original records remain in my possession, and a complete copy of them has been put on file at the Wistar Institute of Anatomy and Biology in Philadelphia, where it may be examined at any time. In the case of the condensed tables which follow, it should be stated here, once for all, that the averages used are always "weighted for the number of cases," while in those instances where it seemed important, there is printed in parentheses along with the average value, the number of measurements on which it is based. The value for the internodes is always given in thousandths of a millimeter (μ).

I. THE AVERAGE LENGTH OF THE INTERNODES AT DIFFERENT LEVELS ALONG THE NERVES TO THE LEG.

As has already been stated, BOYCOTT '04, limited his observations to the average length of the internodes taken from one locality, the distal end of the sciatic nerve. The attempt was therefore made to determine the average length of the internodes at various localities along the nerves supplying the leg.

Fig. 1 gives the arrangement of the nerves to the leg, based on a dissection made by Dr. DUNN '02. The levels from which samples of the nerve were taken are indicated by interruptions in the drawing, and designated by letters, S_1 , S_2 , S_3 , T , T_1 , T_2 , T_3 .

The first four are from the nerve in the thigh, the fifth and sixth from the nerve in the shank, and the seventh from the nerve in the foot.

In each instance a bit of the nerve was prepared according to the method already described, teased as completely as possible, and fifty or more measurements made on the internodes of the fibers, always preferring the larger to the smaller fibers in each instance.

Table 3 gives the results of this sampling; the average at each level being based on the fifty largest fibers which were found.

The method used is sufficiently accurate to justify the statement that on passing peripherally along the nerves to the leg, the fibers of larger diameter become less frequent, and the average

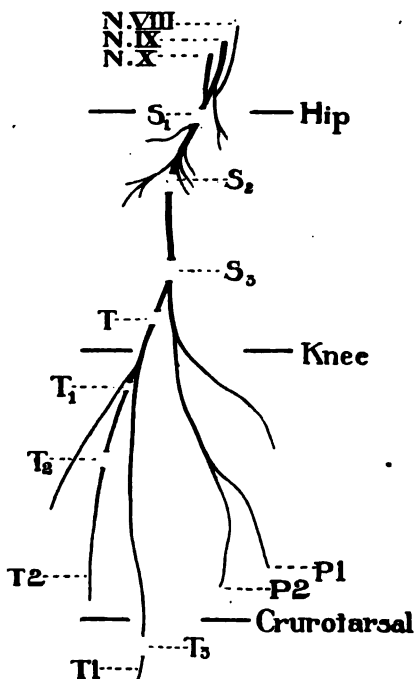


FIG. 1. Giving the main trunks in the nerve to the right leg of the Leopard Frog, as seen from the dorsal aspect. The levels of the several joints are indicated, and also the localities from which pieces of the nerve were taken. These latter are indicated by interruptions, and designated by the letters used in the text. Based on Fig. 1, DUNN '02. P₁, n. peroneus lateralis. T₁, n. tibialis r. superficialis. P₂, n. peroneus medialis. T₂, n. tibialis r. profundus.

length of the internodes diminishes correspondingly. With the exception of the level S₃, in which, owing possibly to the large number of fibers present, the sampling is less representative than at the lower levels, the internodes show a steadily diminishing length as indicated in the last column of Table 3.

The relations of the diameter and the length of the internodes at the several levels are shown in Fig. 2. The levels are indicated

in the figure in their relative positions, and the locations of the hip, knee and crurotarsal joints are shown.

It would follow from this, of course, that if we attempted to determine, as BOYCOTT did, the number of internodes characteristic of the nerve between its origin and any distal point, we should find this number to increase as the sample of the nerve was taken nearer and nearer to the foot. This is exactly what we should

TABLE 3.

Showing the average diameters of the fibers and the lengths of the internodes at the several levels in the nerves to the leg of Frog 6. Body weight, 37 grams; total length, 204 mm. For the identification of the levels, refer to Fig. 1. The number of measurements is given in parentheses above the length of the internodes to which it applies.

Average Diameter in μ Range	5.0	6.6 (6.2-) (7.5)	8.7	10.2 (10.0-) (11.2)	12.0	12.5	12.8	13.1 (13.0-) (13.5)	15.0	16.2	GENERAL AVERAGES.	
											Diam. in μ	Inter- nodes in μ
Levels												
S_1				(13) 987	(15) 1240	(5) 1020		(12) 1225	(4) 1200	(1) 1740	12.1	1154
S_2			(6) 1021	(33) 1111	(9) 1438		(2) 1520				10.4	1175
S_3				(44) 1043	(6) 1283						10.4	1072
T			(2) 938	(40) 1044	(5) 1120		(1) 1051	(2) 1160			10.5	1052
T_1			(20) 816	(30) 793							9.6	802
T_2	(27) 684	(22) 858	(1) 1110								5.8	747
T_3	(34) 588	(16) 731									5.5	632

expect, as Dr. DUNN '02 has shown that the fibers of larger diameter run the shorter courses.

The foregoing result however does not inform us whether the fibers of a given diameter in the same animal have internodes of like length throughout their course. To determine this it is necessary to measure series of fibers of like diameter at different levels, and compare the results with one another. In Frog 6, which furnished the material for Table 3 there is not a sufficient

number of measurements of small fibers at the upper levels to make possible such a comparison. It was therefore necessary to examine other specimens.

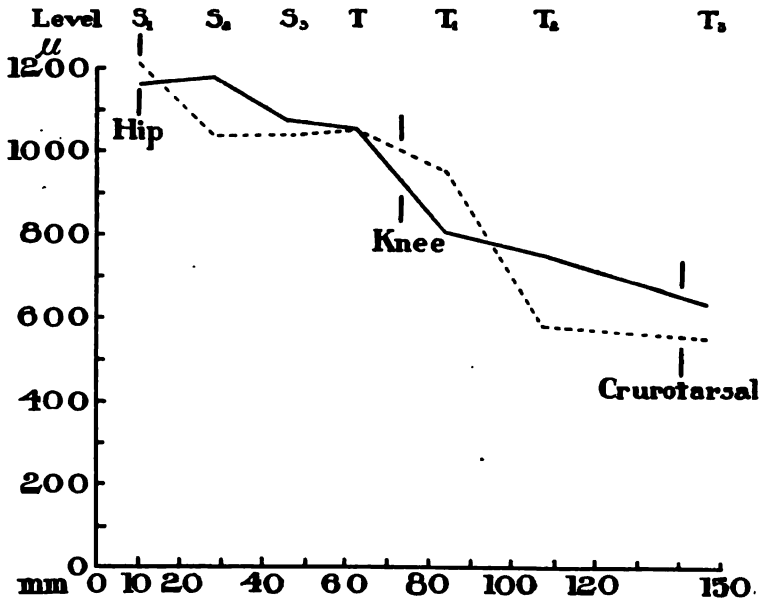


FIG. 2. Showing the average length of the internodes at the several levels in Frog. 6. The values for the diameters have been multiplied by 100, and as this frog is in the growth phase in which the length of the internodes is about 100 times the diameter of the fibers, the two curves run close together. The positions of the hip, knee and crurotarsal joints are also shown.

2. THE LENGTH OF THE INTERNODES AT DIFFERENT LEVELS, ON FIBERS OF LIKE DIAMETER.

For the determination of the length of the internodes at different levels, on fibers of like diameter, Frog 5, weighing 31 grams and having a total length of 192 mm., was used. At each of the seven levels, over 100 internodes on fibers from 5μ to 7.5μ in diameter were measured. For presentation, the fibers have been divided into three classes, having an average diameter of approximately 5.3μ , 6.3μ and 7.3μ , respectively. The results thus condensed are given in the accompanying Table 4.

TABLE 4.

Showing the average length of the internodes on fibers of like diameter at the several levels in the nerves to the leg of Frog 5. Body weight, 31 grams; total length, 192 mm. At each level the measurements are grouped in three classes according to diameter. The number in parentheses indicates the number of measurements.

LEVEL.		INTERNODES.		INTERNODES.		INTERNODES.	
S_1	Diameter.....	5.2 μ (27)	611	6.4 μ (47)	623	7.3 μ (34)	805
S_2	Diameter.....	5.4 μ (42)	645	6.3 μ (38)	706	7.4 μ (40)	889
S_3	Diameter.....	5.3 μ (79)	769	6.3 μ (36)	902	7.2 μ (17)	1000
T	Diameter.....	5.2 μ (38)	646	6.3 μ (30)	787	7.3 μ (50)	836
T_1	Diameter.....	5.2 μ (58)	636	6.4 μ (31)	870	7.4 μ (26)	900
T_2	Diameter.....	5.1 μ (74)	608	6.3 μ (32)	787	7.3 μ (18)	744
T_3	Diameter.....	5.2 μ (72)	818	6.3 μ (25)	917	7.1 μ (9)	1011

When the data in this table are read horizontally, we observe that in all but one instance out of the twenty-one (T_2 , 6.3 μ and 7.3 μ) the fibers with greater diameter have the longer internodes. When the measurements are read vertically however the length of the internodes on a fiber of a given diameter varies irregularly from level to level. Fig. 3 illustrates these relations.

In order to plot these internodal lengths fairly, the diameters of the classes at each level must be made exactly equal, hence they are all reduced for the purposes of this figure to precisely 5.3 μ , 6.3 μ and 7.3 μ . The reduction is made by the method of simple proportion. By reason of this reduction, the internodal values are in some cases slightly different in the figures from those in the tables but at most these differences are slight however and hardly detectable on figures of the size here used.

As it will be necessary for comparison with Tables 6 and 7, to have the measurements from Frog 5 for the levels S_1 , T and T_1 brought together, we now present the data in the accompanying Table 5.

It is to be noted however, in the case of all three diameter classes, that the fibers at T_3 , the level of the foot, give higher values than

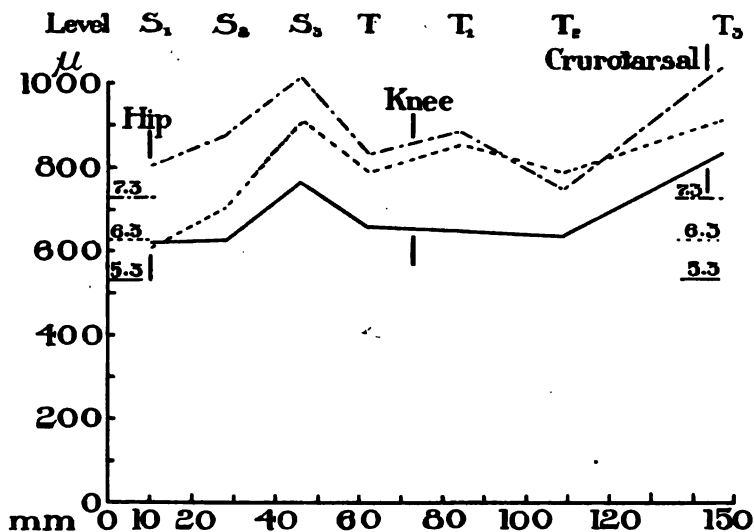


FIG. 3. Showing the average lengths of the internodes at the seven levels in Frog 5. The data for each of the classes has been reduced to the diameters 5.3μ , 6.3μ and 7.3μ . The diameters multiplied by 100 are indicated on the verticals.

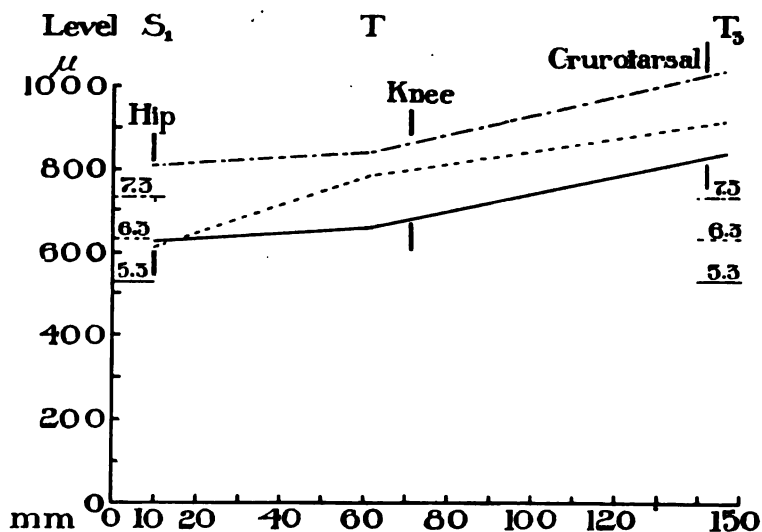


FIG. 4. Showing the average length of the internodes at the levels S , T , and T_3 on the fibers 5.3μ , 6.3μ and 7.3μ from Frog 5. The data are the same as those used in Fig. 3. The diameters multiplied by 100 are indicated on the verticals.

appear at S_1 ; that in the mid-position T and T_1 give intermediate values. This can also be seen by an examination of Fig. 3.

TABLE 5.

Showing the average length of the internodes on fibers of like diameter at the levels S_1 , T and T_1 in the nerves to the leg of Frog 5. Otherwise, this table is similar to Table 4.

LEVEL.		INTERNODES.		INTERNODES.		INTERNODES.	
S_1	Diameter.....	5.2 μ (27)	611	6.4 μ (47)	623	7.3 μ (34)	805
T	Diameter.....	5.2 μ (38)	646	6.3 μ (30)	787	7.3 μ (50)	836
T_1	Diameter.....	5.2 μ (72)	818	6.3 μ (25)	917	7.1 μ (9)	1011

In view of this result, it was thought necessary to determine this same relation in other specimens. Before commenting on the foregoing results, therefore, the additional observations on this point will be presented.

A large specimen, Frog 8, body weight 63 grams, total length 222 mm., was examined. Three localities on the nerves to the leg, namely S_1 , T and T_1 , were selected, and more than 100 internodes measured at each level. The measurements were made on fibers from 5 μ to 7.5 μ in diameter. These have been arranged as before, in three classes, approximately 5.3 μ , 6.3 μ and 7.3 μ in diameter, and the data thus condensed, are given in Table 6.

TABLE 6.

Showing the average length of the internodes at the several levels in the nerves to the leg of Frog 8. Body weight, 63 grams; total length, 222 mm. At each level, the measurements are grouped in three classes according to diameter. The numbers in parentheses indicate the number of measurements.

LEVEL.		INTERNODES.		INTERNODES.		INTERNODES.	
S_1	Diameter.....	5.3 μ (45)	711	6.3 μ (31)	828	7.5 μ (44)	909
T	Diameter.....	5.1 μ (61)	589	6.4 μ (33)	723	7.4 μ (44)	923
T_1	Diameter.....	5.1 μ (79)	806	6.3 μ (56)	963	7.4 μ (48)	1015

When read horizontally, the records in Table 6 show that the length of the internodes increases with the increasing diameter of the fibers. When read vertically however it appears that while at T , the internodes are always longer than at S_1 , yet the internodes for fibers with the diameters 5.3μ and 6.3μ at the level T are shorter than those either above or below this level. Comment on this result will be made later.

Fig. 5 also represents these relations, the measurements at all three levels having been reduced to exactly the same diameter, namely, 5.3μ , 6.3μ and 7.3μ .

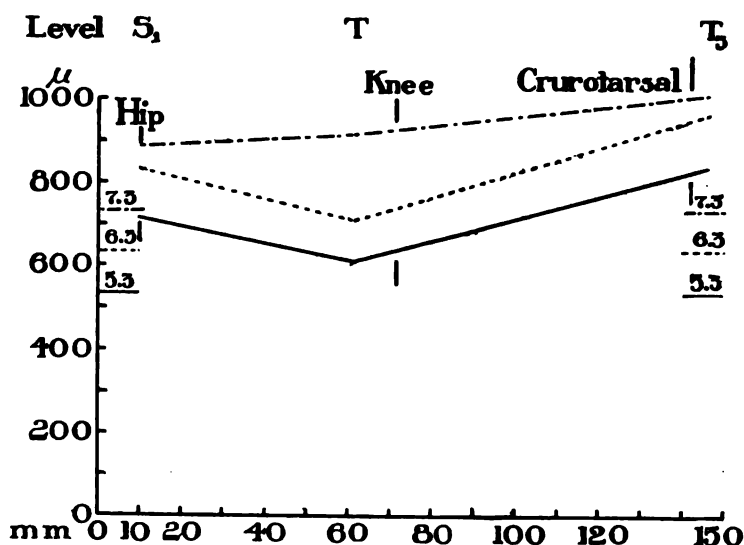


FIG. 5. Showing the lengths of the internodes at the levels S_1 , T , and T_2 , on fibers 5.3μ , 6.3μ and 7.3μ in diameter from Frog 8. The diameters multiplied by 100 are indicated on the limiting verticals.

In addition to Frog 8, still another specimen, Frog 3, body weight 26 grams, total length 166 mm., was examined in the same way. More than 100 internodes on fibers ranging in diameter from 3.75μ to 6.3μ were measured at each of the three levels S_1 , T and T_2 .

The measurements are treated as before, and are presented in Table 7.

The table reads regularly, both horizontally and vertically, and thus shows a steady increase in the length of the internodes, as

the fibers increase in diameter, and also along a given fiber from S_1 towards the foot T_3 .

TABLE 7.

Showing the average length of the internodes at the several levels in the nerves to the leg of Frog 3. Body weight, 26 grams; total length, 166 mm. At each level the measurements are grouped in three classes according to diameter. The numbers in parentheses indicate the number of measurements.

LEVEL.		INTERNODES.		INTERNODES.		INTERNODES.	
S_1	Diameter.....	3.9 μ (12)	416	5.2 μ (72)	520	6.3 μ (25)	578
T	Diameter.....	4.0 μ (13)	435	5.2 μ (64)	601	6.3 μ (23)	692
T_3	Diameter.....	4.0 μ (24)	578	5.2 μ (53)	701	6.3 μ (63)	805

Fig. 6 exhibits these relations in the form of curves.

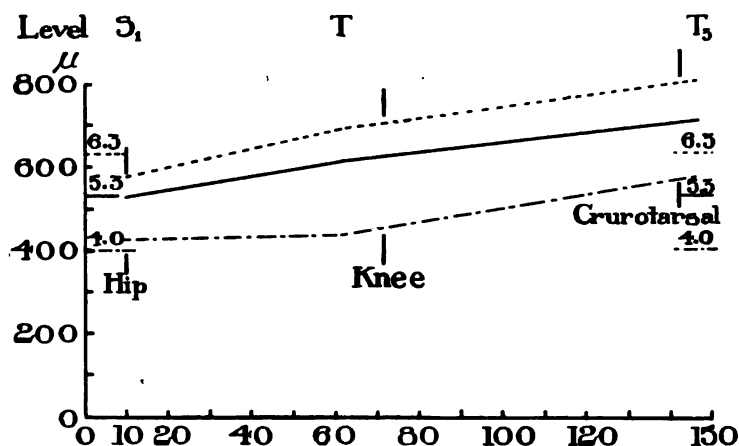


FIG. 6. Showing the average length of the internodes at the several levels, S_1 , T and T_3 , on fibers 4 μ , 5.3 μ and 6.3 μ in diameter, from Frog 3. The other indications as in Fig. 5.

As the foregoing represents all the data collected in connection with this question, we return to a discussion of the fundamental point, namely, the length of the internodes on fibers of a given diameter through their entire extent from S_1 towards the foot T_3 . An examination of Tables 5, 6 and 7 shows:

First, that on fibers of a given diameter, the internodes are not of the same lengths at the several levels;

Second, that in general, the internodes become longer as we pass toward the periphery;

Third, that they are markedly elongated at T_{II} , the level of the foot.

In attempting to explain these relations, we naturally call to mind the fact that in *Rana pipiens*, the average proportional lengths of the leg bones are

Femur.....	26.1
Tibia.....	29.6
Tarsus and pes	44.3

These figures are the averages from Table XI in DONALDSON and SCHOEMAKER '00.

As these relative values remain practically unchanged during the growth of the leg in length, it follows that the increments in length must be in the same proportion, and therefore a lengthening of 100 units in the femur, is accompanied by a lengthening of 113.4 units in the tibia, and 169.7 units in the tarsus and pes. If, for the moment, we assume that the portion of the nerve in each segment of the limb is so linked with that segment that it lengthens at the same rate, then we should expect a corresponding relation in the length of the internodes; provided, of course, they were of equal length when first laid down. It appears worth while to put this conclusion to the test, so far as the data in hand will permit.

Before this can be done however several adjustments and corrections must be made in the raw values. In the first place, as the intermediate level T is within the limits of the thigh, and hence associated with the femur, the measurements at T are excluded from the following comparisons, and we contrast only the length of the internodes at S_1 with that found at T_{II} , to determine whether these lengths stand in the same relation as the increments of growth in these segments of the limb, namely, as 100 : 169.7. In order to do this, it is necessary to compare the internodal lengths belonging to classes of fibers having exactly the same diameters. We choose as the standards for the diameter classes, 4μ , 5.3μ , 6.3μ and 7.3μ , since the observed values can be reduced to these standards by alterations which never amount to more than $.2\mu$.

In doing this, we assume that the reduction can be made by simple proportion. The results based on the reduced values are given in the following Table 8.

TABLE 8.

Showing the relative length of the internodes at T_2 , compared with those at S_1 as a standard, in the case of the several diameter classes in all three frogs (Frog 3, Frog 5 and Frog 8).

	DIAMETER IN μ .	INTERNODES AT		RELATIVE VALUE AT T_2 FOR EACH DIAMETER CLASS.	RELATIVE VALUE AT T_2 . AVERAGE FOR EACH FROG.
		S_1	T_2		
Frog 3.....	4.0	425	578	136.0	136.6
	5.3	530	714	134.7	
	6.3	578	805	139.2	
Frog 5.....	5.3	623	834	133.8	134.6
	6.3	645	917	140.9	
	7.3	805	1039	129.1	
Frog 8.....	5.3	711	837	117.7	115.7
	6.3	828	963	116.3	
	7.3	885	1001	113.3	

A study of Table 8 reveals several points of interest. First, the internodes at T_2 are always considerably longer than at S_1 .

Second, the relative value at T_2 , ranging from 136.6 to 115.7, is always much less than the relative growth of the foot, namely, 169.7.

Third, it appears that this proportional excess of the internodes in the foot tends to diminish in the larger frogs. Frog 8, the largest, showing a value of 115.7, whereas Frog 3, the smallest frog, shows 136.6, and Frog 5, intermediate in weight and length, gives an intermediate value.

We conclude from these relations, that while the length of the internode along the fiber is probably influenced by the elongation of the segment in which it is found the effect of the local elongation is more or less distributed over the entire length of the nerve fiber. If we wish therefore to discover what is really taking place as regards the lengthening of the internodes, we must study the changes over the entire extent of the fiber.

For this purpose it is necessary to determine the average lengthening of the internodes during the period of growth on the nerve fibers taken from Frog 3, Frog 5, and Frog 8. To do this fairly, the diameter classes must be made exactly similar. In addition, due account must be taken of the fact that not only do the internodes increase in length, but the fibers to which they belong, increase at the same time in diameter, and therefore a diameter class of given size in the smaller frog must always be compared with a class of greater diameter in the larger frog. To make this, comparison it is necessary to obtain some notion of the amount of change in diameter which may be expected to occur in the cases we are examining.

Finally, for comparison, it is necessary to determine in the several frogs compared the proportional lengthening of the nerves to which these fibers belong.

In the absence of direct observations, we assume that the lengthening of the fibers which pass from the intervertebral foramina to the foot, is proportional to the lengthening of the leg itself. To determine what this is, we proceed as follows:

Since in the case of the frogs in question, the length of the legs is always a constant fraction of the total length of the frog, it follows that the increase in the length of the legs will be in proportion to the increase in the total length of the frog.

Treating the data in this way, we obtain the results shown in Table 9.

TABLE 9.

Showing the relative length of the legs in Frog 3, Frog 5, and Frog 8, based on a comparison of the total lengths of these same frogs. Group (A). Frog 3 taken as the standard. Group (B). Frog 5 taken as the standard.

FROG.		TOTAL LENGTH.	RATIO FOR THE LEGS.
		<i>mm.</i>	
Group (A) {	3.....	166	100.0
	5.....	192	115.6
	8.....	222	133.7
Group (B) {	5.....	192	100.0
	8.....	222	115.6

From Table 9 it appears that when Frog 3 is taken as the standard in Group (A) the length of the leg in Frog 5, is 15.6 per cent greater, and in Frog 8, 33.7 per cent greater, while in the second

instance, Group (B) where Frog 5 is taken as the standard, the leg in Frog 8 is 15.6 per cent greater.

Our next step is to make an approximate determination of the increase in the diameter of the growing fibers in the frogs in which the nerves to the leg increase 15.6 per cent over the standard.

To determine the increase in diameter which probably occurs when the nerve increases 15.6 per cent in length, we proceeded as follows:

By comparing the sum of the internodal lengths of the 4μ , 5μ and 6μ fibers in Group I of BOYCOTT's table (reprinted as Table I on p. 168) with the corresponding sum of the 5μ , 6μ and 7μ fibers in Group II and these in turn with the sum of the 6μ , 7μ and 8μ fibers in Group III, it was found that for an increase of 1μ in diameter, there was an average increase in internodal length of 25.9 per cent. Since we assume in the case of our own frogs that the internodal length will increase in proportion to the increase in the length of the nerve, and since the latter amounts to 15.6 per cent, it follows that if an increase of 25.9 per cent in internodal length, calls for an increase of 1μ in the diameter of the fiber, then 15.6 per cent increase in internodal length, will call for approximately 0.6μ increase in the diameter of the fiber.

This result is based of course on BOYCOTT's measurements made on *R. temporaria*. It seems justifiable to apply it to *R. pipiens* however because, although DONALDSON '08 has shown that the internodes in *R. pipiens* are shorter than in *R. temporaria*, he has also shown that the proportional differences in length are nearly the same for the several diameter classes, and hence any given change in the diameter, is associated with the same relative change in length of internode in both species.

Accepting therefore this determination of the diameter increase, the next step is to compare the internodes on the fibers of a given diameter of one specimen of *R. pipiens*, with the internodes in another specimen, on fibers which are 0.6μ greater in diameter. To do this, we select from the foregoing Tables 5, 6 and 7, the internodal lengths on fibers for the diameter classes 5.3μ , 6.3μ and 7.3μ from all three levels. This permits us to make nine comparisons.

Thus in each of these comparisons, as for instance in the first one, in Table 10 the average internodal length in the diameter class 5.3μ at S_1 in Frog 3, is compared with the average internodal

length on fibers 5.9μ in diameter at S_1 in Frog 5, and the same procedure is followed in each of the other eight comparisons.

The foregoing tables, 5, 6 and 7, however, show the internodal values only for the diameter classes 6.3μ and 7.3μ , while for our present purpose, it is necessary to use those for 5.9μ and 6.9μ . The desired values are obtained by the simple proportional reduction of the internodal length of the 6.3μ class to that for 5.9μ , and of the 7.3μ class to that for 6.9μ .

In view of all conditions, the values thus determined, are probably nearly correct, although the method is open to some theoretical objections. The comparisons which are thus made possible are given in Table 10.

TABLE 10.

Showing the growth of the internodes on the fibers 5.3μ and 6.3μ in diameter, in nerves which increase 15.6 per cent in length. Internodes from Frog 3, compared with those from Frog 5, and from Frog 5 compared with those from Frog 8.

LEVEL.	FROG.	DIAMETER IN μ .	INTERNODES.	PERCENTAGE INCREASE.	AVERAGE PERCENTAGE INCREASE FOR EACH LEVEL.
S_1	3	5.3	530		
	5	5.9	596	12.4	
	5	5.3	623		
	8	5.9	773	24.1	
	5	6.3	635		
	8	6.9	834	31.0	22.5
T	3	5.3	601		
	5	5.9	738	22.7	
	5	5.3	646		
	8	5.9	667	3.2	
	5	6.3	787		
	8	6.9	863	9.6	11.8
T_2	3	5.3	714		
	5	5.9	856	20.0	
	5	5.3	834		
	8	5.9	903	8.2	
	5	6.3	917		
	8	6.9	945	3.0	10.4

As Table 10 shows, the average growth of the internodes at S_1 is 22.5 per cent, which is greater than that at T , 11.8 per cent, or at T_2 , 10.4 per cent. Also the percentage increase at the level S_1 is greater in the larger than in the smaller frogs. These results accord with those previously noted in the examination of the internodal lengths on fibers from the same frogs, in which the length of the internodes in the foot becomes proportionally less as the frog becomes larger (see Table 8).

To determine the average growth of the internodes on individual fibers, it is necessary to measure the fibers of a given diameter class taken from the same frog, at all three levels, and Table 11, based on the data in Table 10, gives the values found.

TABLE 11.

Showing the percentage increase in the average length of the internodes on fibers of a given diameter, when all three levels from the same frog are included. The averages used are those given in Table 10.

	Frog 3	Frog 5	Frog 5
Diameter.....	5.3 μ	5.3 μ	6.3 μ
S_1	12.4	24.1	31.0
T	22.7	3.2	9.6
T_2	20.0	8.2	3.0
Averages for each frog.....	18.4	11.8	14.5
Grand average.....	14.9 per cent increase.		

It is seen from the foregoing, that the average increase in the length of the internodes in Frog 3, fibers 5.3 μ in diameter, is 18.4 per cent, Frog 5, fibers 5.3 μ in diameter, 11.8 per cent, and Frog 5, fibers 6.3 μ in diameter, 14.5 per cent; the grand average for the three frogs being 14.9 per cent. The nerves to which these fibers belong have lengthened in each case 15.6 per cent, so that the accordance is fair in each instance, except in the case of the 5.3 μ group in Frog 5. It should be recalled however that in the 6.3 μ group in Frog 8, at the level T , a very low value was obtained (Table 6). Because this value is less than that at S_1 , it may be considered aberrant, and it is the presence of this value which causes the low percentage, 3.2 per cent, in Frog 5, at the level T . If this observation is excluded, the value for the 5.3 μ group in

Frog 5 becomes 16.1 per cent or nearly that for the lengthening of the nerve, and the grand average becomes 16.4 per cent, or a little greater than 15.6 per cent, which represents the lengthening of the nerve.

It seems allowable therefore to conclude that the internodes in the 5.3μ and 6.3μ diameter classes, grow, on the average, at approximately the same rate as does the nerve in which they are found. Nevertheless on passing distally along the nerve, the length of the internodes in a given diameter class, tends to increase in such a way as to suggest that it is influenced by the growth of the segment of the limb to which the internodes belong, although this influence becomes less marked as the frog becomes larger.

3 THE LENGTH OF THE INTERNODES ON FIBERS IN THE ROOTS OF THE SPINAL NERVES.

Touching this point we have observations on the roots of the IX nerve in five frogs of different sizes. In his plate VI, HARDESTY ('99) has given some excellent drawings of the nerve roots in this frog. The species used by HARDESTY was designated *Rana virescens* but is the same as that here designated, *Rana pipiens* (see DONALDSON '07).

The present data are brought together in Table 12. Each specimen is given the number which it bears in Table 2 but the series is arranged in the order of the increasing length of the nerve roots.

Table 12 shows that as the nerve roots increase in length, the internodes on the fibers in these roots also increase in length. The average length of the internodes is somewhat less in the dorsal roots than in the ventral, and this, in each instance, goes along with a smaller average diameter of the fibers measured. Fig. 7 shows these relations also.

Using the data in Table 12, we may form the supplementary Table 13 in which are compared the values for the length of the ventral or dorsal root, with the corresponding values for the internodes on fibers in this root. The series of ratios given in Table 13 indicate that the internodes on fibers of both roots lengthen in about the same proportions as the roots in which they appear. It is interesting to observe that this lengthening of the roots is quite independent of the increase either in the total length, or in

the body length, of the frogs concerned. It appears from this, that the internodes on the roots of the IX nerve grow as do the internodes in the nerve to the leg. Concerning the limits of the stretch of nerve which we have to examine, we may feel very sure that in the case of the dorsal root they have been correctly determined. This stretch lies between the spinal ganglion and the point of union of the root with the cord. In the case of the ventral root however the corresponding stretch appears to be between the cord as one limit and the junction of the ventral with the dorsal root as the other, although further observations are necessary to establish the latter limit beyond dispute.

TABLE 12.

Showing the length of the nerve roots of the IX nerve, and the average length of the internodes on the fibers in them. The averages were obtained from random sampling and are based on the measurement of 50 fibers in each case.

SERIAL NUMBER FROM TABLE 2.	SEX.	BODY WEIGHT.	1 TOTAL LENGTH 2 BODY LENGTH.	LENGTH OF V (VENTRAL) D (DORSAL) ROOTS.	DIAMETER OF FIBERS. VENTRAL ROOT.	LENGTH OF INTERNODES. VENTRAL ROOT.	DIAMETER OF FIBERS. DORSAL ROOT.	LENGTH OF INTERNODES. DORSAL ROOT.
		grms.	mm.	mm.	μ		μ	
1	M.	5.5	10.4	V 2.6	8.6	389	6.4	303
8	M.	63.0	3.9	D 2.1				
			222.0	V 5.9	11.2	1054	10.2	961
			89.4	D 5.4				
2	M.	23.5	169.0	V 7.0	14.4	1131	11.7	955
			71.0	D 6.5				
4	F.	27.2	180.0	V 7.7	13.6	1325	12.1	1116
			78.0	D 7.1				
7	M.	61.1	226.0	V 9.5	14.7	1339	11.0	1153
			89.0	D 9.0				

In the relations between the diameter of the fibers and the length of the internodes in the dorsal and ventral roots, there are certainly no striking differences, since in the ventral roots the internodal length is on the average 84 times the diameter, while in the dorsal roots it is 87 times. If we compare the length of the internodes on fibers of a given diameter in the ventral and dorsal root and also in the sciatic nerve at the level S_1 in Frog 8—the only specimen in which the comparison can be made—it appears that

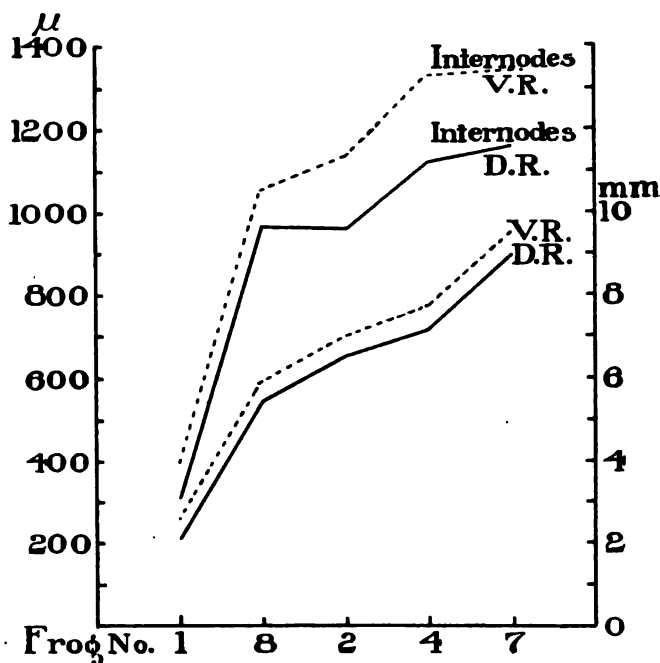


FIG. 7. To show the length of the dorsal (D.R.) and ventral (V.R.) roots respectively, in the IX nerve of the five frogs examined, and the corresponding lengths of the internodes on fibers from these roots, the measurements for the roots are given in millimeters on the vertical to the right, and for the internodes in μ , on the vertical to the left.

TABLE 13.

Based on data in Table 12 and comparing the relative increase in the length of the nerve roots with the relative increase in the length of the internodes as shown by a series of ratios.

SPECIMENS.	VENTRAL ROOTS.		DORSAL ROOTS.	
	RATIOS OF LENGTH OF ROOTS.	RATIOS OF LENGTH OF INTERNODES.	RATIOS OF LENGTH OF ROOTS.	RATIOS OF LENGTH OF INTERNODES.
Frog 1.....	1.00	1.00	1.00	1.00
Average of Frogs 8 and 2...	2.48	2.80	2.83	3.16
Average of Frogs 4 and 7...	3.31	3.42	3.83	3.74

the internodal lengths are greater in the sciatic than in the spinal roots. These values are given in Table 14.

TABLE 14

Showing in Frog 8 the lengths of the internodes on fibers 10μ , 11.25μ and 12.5μ in diameter from the ventral and dorsal roots of the IX nerve, and from the sciatic at the level S_1 . The numbers in parentheses indicate the number of measurements made in each case, and apply to the internodal value above which they are placed.

DIAMETERS IN μ	INTERNODAL LENGTHS.		
	IX NERVE VENTRAL ROOT.	IX NERVE DORSAL ROOT.	SCIATIC NERVE LEVEL S_1 .
10.00	(28) 1064 (24)	(16) 1037 (12)	(46) 1147 (11)
11.25	1018 (24)	910 (10)	1238 (51)
12.50	1110	1015	1316

Just what interpretation is to be given to the difference in the internodal lengths, from these several localities, must await the collection of a much larger number of observations.

We turn next to the comparison of the length of the internodes in the III, with those in the IX spinal nerve. Owing to the technical difficulties already mentioned, p. 171, we have only a limited number of observations on the ventral root of the III nerve of Frog 2, to be compared with those on the fibers in the ventral root of the IX nerve from the same frog. If we select the fibers 10μ to 15μ in diameter, inclusive, and tabulate the average values of the internodes for each diameter class, we get the results presented in Table 15.

TABLE 15.

Giving the length of the internodes on fibers 10μ to 15μ in diameter, in the ventral roots of both the III nerve and IX nerve of Frog 2. The numbers in parentheses indicate the number of observations.

DIAMETERS IN μ	10	11.25	11.6	12.5	13.33	13.75	14.16	15
III nerve.....	(12) 960	(8) 1052		(17) 1050		(2) 1210		(2) 1440
IX.....	(2) 980		(1) 940	(8) 985	(1) 1000	(9) 1220	(2) 1130	(26) 1147

An examination of Table 15 shows that for fibers of the same diameter, the internodal lengths are nearly alike in the two nerves. If we make a general average, we find the relations given in Table 16.

TABLE 16.

Giving the average diameters and average length of internodes on the fibers from 10μ to 15μ in diameter, found in the ventral roots of the III and IX nerves of Frog 2.

	DIAMETER IN μ .	INTERNODAL LENGTH.
Nerve III.....	11.7	1051
Nerve IX.....	14.0	1117

In view of the small number of observations, we may look upon these values as similar, but the fact that they are similar, is the surprising result, since in this particular case (see Table 12) the length of the ventral root of the III nerve is 2.6 mm., while that of the IX nerve is 7.0 mm., giving a ratio of 1 : 2.7. If we assume that these roots had the same length when medullation began, it would appear that since the IX nerve had become 2.7 times as long as the III, the internodes should stand in a like relation.

The measurements show that such is not the case. Unfortunately, at the moment, it is not possible to explain this result. The discrepancy possibly arises through taking as the distal limit of the ventral roots the point of junction of the ventral with the dorsal root, and yet the assumption of this limit fitted perfectly with what has already been found in the case of the IX nerve. There are of course many suggestions which might be made, but it seems best to leave the question in abeyance, until a larger number of observations, especially on the dorsal root of the III nerve, has been made.

4 THE NUMBER OF MEDULLATED FIBERS AT DIFFERENT LEVELS IN THE LEGS OF TADPOLES OF INCREASING SIZE.

To fill out our information as to the way the medullary sheaths of the nerve fibers are acquired in the frog, the number of the medullated fibers at the level of the knee was counted, and compared with the number at the entrance to the foot, in the legs of tadpoles of increasing size. To prepare this material, the legs, or so much

of them as was needed, were fixed in 1 per cent osmic acid, and then embedded and sectioned in the usual manner. The sections were made 12μ in thickness, and at the knee, the number of medullated fibers in the trunks of the nervus tibialis and nervus peroneus was counted. This number was contrasted with that found in the four trunks entering the foot, namely: the ramus superficialis and ramus profundus of the nervus tibialis, and the nervus peroneus lateralis and medialis.

At both levels the number of fibers in several successive sections was counted, and the average taken. The results of this examination are presented in Table 17.

TABLE 17

Showing the number of medullated fibers at the level of the knee and ankle in the leg of the tadpole. Tadpoles of *Rana pipiens*.

NUMBER OF SPECIMEN.	LENGTH OF SHANK	LENGTH OF FOOT.	NUMBER OF FIBERS IN A CROSS SECTION AT THE LEVEL OF		RATIOS OF NUMBER AT KNEE TO NUMBER AT ANKLE.
			KNEE.	ANKLE.	
	mm.	mm.			
I	1.18	0.68	23	4	5.75-1
II	1.29	0.80	25	6	4.16-1
III	1.50	0.96	30	8	3.75-1
IV	1.88	1.36	85	25	3.40-1
V	3.68	2.71	286	118	2.42-1

It appears from this that both the absolute and relative number of medullated fibers entering the foot, increases as the leg of the tadpole becomes longer, rising from 1 : 5.75 to 1 : 2.42. In a large mature frog, Dr. DUNN ('02) has shown that the ratio is 1 : 1.66, an increase of $3\frac{1}{2}$ fold over the ratio in the smallest tadpole. At the moment however we have no data by which to determine when the ratio found in the largest tadpole's leg here examined passes over to that in the mature frog.

It is assumed that the medullated fibers which are counted at the level of the knee, represent fibers already medullated throughout their entire length, as well as fibers incompletely medullated, but having a sheath extending as far as the level of the section. The same assumption is made for the fibers at the level of the foot.

It is shown then that the medullation of fibers going to the shank, the more proximal segment of the limb, is more nearly complete than that of those passing to the foot, the more distal segment, and probably the greater part of this difference depends upon the fact that many of the fibers destined for the foot are not medullated at all.

This result, taken in conjunction with those of HARDESTY ('99) on the nerve roots of the frog, and HATAI ('01, '02), on the nerve roots of the rat, indicates very clearly that new medullated fibers are continually being added to the nerves during the period of growth.

5 A COMPARISON OF THE LENGTH OF THE INTERNODES IN THE AMERICAN LEOPARD FROG, *RANA PAPIENS*, WITH THEIR LENGTH IN THE ENGLISH FROG, *RANA TEMPORARIA* (*FUSCA*).

In his study, entitled "The nervous system of the American leopard frog, *Rana pipiens*, compared with that of the European frogs, *Rana esculenta* and *Rana temporaria* (*fusca*)," Dr. DONALDSON ('08) compared the measurements of the internodes made by me on *Rana pipiens*, with those made by BOYCOTT on *Rana temporaria*. Taking the same locality in both cases, and reducing the measurements on *R. pipiens* so that they apply to frogs of the same total length as those measured by BOYCOTT, a series of values was obtained for seven diameter groups. It appeared from a comparison of the results (see DONALDSON '08, p. 146, Table 19), that the internodal lengths in *Rana pipiens*, ranged between 64 and 71 per cent of those found in *Rana temporaria*, the average being 67 per cent.

The comparison appears to be a fair one, and if this is granted, it is evident that *Rana pipiens* has on its fibers three sheathing cells, where *Rana temporaria* has two. This result further draws attention to the fact that the character in question is subject to considerable variation, and that this appears not only in forms widely separated zoologically, but also within the genus *Rana*, at least in the case of the two closely related species here compared.

CONCLUSIONS.

In the leopard frog, *Rana pipiens*, we have found:

1. The average length of the internodes on the fibers in the nerves to the leg diminishes towards the periphery. This diminution is accompanied by a corresponding diminution in the average diameter.

2. In the same frog, the length of the internodes at different levels on fibers of like diameter in the nerves to the leg, *increases* toward the periphery. This increase appears to be associated with the more rapid growth of the distal segments of the leg, but the influence of the segment on the portion of the nerve within it, is less marked as the frogs become larger.

3. When the average length of the internodes on fibers of a given diameter is compared with the average length on the fibers which represent them in a larger frog, it is found that the lengthening of the internodes corresponds with that of the nerve to which they belong, thus supporting BOYCOTT's ('04) general conclusion.

4. In the roots of the IX spinal nerve, the internodes lengthen in proportion to the lengthening of the nerve, but at the same time, the lengthening of these roots is only loosely correlated with the increase either in the total length or in the body length of the frog to which they belong.

5. When, in the same frog, the ventral root of the III nerve is compared with the ventral root of the IX nerve, it is found in both of them, that the fibers of the same diameter have internodes of the same length. In the case chosen, the ventral root of the IX nerve had become 2.7 times the length of the III nerve and we should therefore expect to find the internodes on the fibers of the IX nerve much longer than those on the corresponding fibers in the nerve III. The explanation of this result awaits further observations.

6. A determination of the number of medullated nerve fibers at the level of the knee and of the ankle in a series of tadpoles' legs of increasing length, shows that the relative number of medullated fibers at the ankle, increases as the leg becomes longer, thus proving that the fibers to the more distal divisions of the limb are medullated later.

7. It follows from the foregoing result that so long as the nerve receives new (young) fibers, there will always be internodes which

are relatively short, since they belong to fibers which have been subjected to the lengthening process for only a short time. The presence of these fibers reduces the average length of the internodes, and hence accounts in part at least, for BOYCOTT's observation that on the average the lengthening of the internodes in the sciatic nerve is slightly less than that of the nerve itself. It also accounts, in part at least, for the wide range in the length of the internodes found on fibers of the same diameter.

8. In the leopard frog, *Rana pipiens*, the length of the internodes at the distal end of the sciatic nerve, is on the average, only about two-thirds that of the corresponding internodes in *Rana temporaria* (*fusca*) as measured by BOYCOTT ('04).

SUMMARY.

The foregoing conclusions may be made more vivid perhaps if, in the light of our present knowledge, we attempt to picture the growth changes which affect the internodes on the nerve fibers of the leopard frog. From the observations of HIS ('86) HARRISON ('01, '04-'06), BARDEEN ('02-'03), and others, we know that the axone grows out from the cell body into the peripheral nerve, accompanied by its sheathing cells. There are no observations to show whether before the formation of the myelin the sheathing cells cover approximately the same length of fiber in all fibers, or at all periods of growth, but our observations as they stand, would favor such a view.

In the leg of the tadpole, the formation of myelin occurs first in the fibers which run the shorter course, and interpreting the findings of HARDESTY ('99) and HATAI ('03) showing a diminishing number of medullated fibers in the spinal roots as we pass away from the cells of origin, it appears that the development of the myelin progresses from the cell of origin toward the end of the axone.

When the axone has made its distal connection, and the myelin is formed, then the lengthening begins, and continues so long as the nerve to which the fiber belongs, continues to grow. In the nerves to the leg however this process is modified by the fact that the internodes have a tendency to lengthen at the same rate as the segment of the leg to which they belong; although this process is more marked in the younger than in the older frogs. Despite this

however the average length of the internodes on fibers of a given diameter increases as does the nerve in which they occur.

The interpretation of the internodes, as we find them in a sample taken from any nerve, is complicated by the fact that for a long time during growth, new medullated fibers are appearing. As these new fibers start with very short internodes, and are late in appearing, they have been affected by the lengthening process for a shorter time than those fibers which were completely medullated at an earlier date. They must consequently exhibit internodal lengths shorter than would be expected, and since their absolute number increases as the frog becomes larger, and their presence lowers the average length of the internodes at any level, it will necessarily follow, as shown by BOYCOTT ('04), that the average length of the internodes increases a little less rapidly than that of the nerve to which they belong. This is our explanation of BOYCOTT's result.

While this change in the length of the internodes is taking place, there is also a change in the diameter of the fibers. In general, the increase in diameter is in advance of the increase in internodal length, so that, as BOYCOTT has shown, fibers of a given diameter have longer internodes in larger frogs.

The exact relation of these two processes has still to be worked out, but this relation, depending as it does on the medullation of the fibers at different dates, and on the fact that all fibers of small diameter are not destined to become fibers of large diameter (BOUGHTON '06), but may remain permanently small, seems to account for the great variation in the length of the internodes on fibers of the same diameter, quite aside from the fact that consecutive internodes on the same fiber may have very different lengths.

While the foregoing description is based on the study of the nerve to the frog's leg, we find that it applies also to the growth changes in the roots of the IX spinal nerve, when we take as the limits of the dorsal root, the spinal ganglion on one side, and the spinal cord on the other, and in the case of the ventral root, the spinal cord on one side, and the junction point of the ventral and dorsal roots on the other.

When however we compare the internodal lengths in the IX ventral root with those in the III ventral root of the same frog, taking the same limits, we get the surprising result that the internodal lengths are similar, although the lengthening of the IX nerve

has been 2.7 times that of the III. This result still awaits an explanation.

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THE BEHAVIOR OF THE LARVAL AND ADOLESCENT STAGES OF THE AMERICAN LOBSTER (*HOMARUS AMERICANUS*).¹

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Commission of Inland Fisheries.)*

WITH TWENTY-TWO FIGURES.

OUTLINE OF CONTENTS.

I. INTRODUCTION AND HISTORICAL SUMMARY.....	200
II. BIOLOGY OF THE LOBSTER.....	203
III. APPARATUS AND METHOD OF PROCEDURE.....	205
IV. PRELIMINARY EXPERIMENTS.....	208
V. SYSTEMATIC ACCOUNT OF THE REACTIONS TO LIGHT OF LOBSTERS IN THE LARVAL STAGES ..	216
1. First larval stage.....	217
2. Second larval stage.....	228
3. Third larval stage.....	232
4. Fourth stage.....	241
5. Fifth stage.....	248
A. Photopathy versus phototaxis.....	250
B. Phototaxis leading to fatal results.....	251
C. Conclusions concerning the reactions to light of fifth-stage lobsters.....	253
D. Contact-irritability versus reaction to light.....	253
VI. MECHANICS OF ORIENTATION.....	258
1. The normal behavior of the larvæ.....	258
2. Mechanics of progressive orientation.....	261
3. Mechanics of body-orientation.....	263
A. The effect of direct lighting and shading.....	264
B. The effect of screens and backgrounds.....	277
VII. ANALYSIS.....	289
VIII. SUMMARY.....	298
IX. LIST OF REFERENCES.....	300

¹ The present paper is the last of the series of four in which the author has attempted to analyze the behavior of the larval and early adolescent stages of the lobster. The papers already published are the following, references to which may be found in the bibliography at the end of the present work: (1) The relation of optical stimuli to rheotaxis in the American lobster; (2) Galvanotaxis in larvæ of the American lobster; (3) The reaction of blinded lobsters to light.

I. INTRODUCTION AND HISTORICAL SUMMARY.

Every year is bringing new and valuable additions to our knowledge of the behavior of the Crustacea. Most of the investigations dealing with this subject are concerned, however, with the Entomostraca, while the behavior of the higher forms has been less studied. It is apparent, moreover, that the experimental work done has been chiefly upon adults, while little attention has been given to the behavior of the larval forms of those Crustacea, as the macrurous decapods, which undergo an extensive metamorphosis. It is the aim of the present paper to demonstrate certain phases in the reactions of larval and early adolescent stages of the American lobster (*Homarus americanus*) to light, and to analyze these reactions, so far as possible, into their constituent factors.

In the study of reactions to light it is apparent that the lack of a satisfactory terminology has led to considerable confusion. This is manifest when we attempt to apply the definition of positive or negative phototaxis, as given by LOEB, to the types of behavior which we find, for instance, in the lobster and in the shrimp, *Palemonetes* (LYON 1907). LOEB (1905, p. 29) states that "positively heliotropic animals are compelled to turn their oral pole toward the source of light and move in the direction of the rays to its source." In the larval lobsters, however, there may be a difference between the signs of body-orientation and what may be called progressive orientation. In body-orientation the animal in question *turns* with reference to the source of light; in progressive orientation it moves toward or from the source of light. Employing these terms, we may say that the body-orientation of the larval lobster under stimulation by light is invariably negative, whereas the progressive orientation may be either positive or negative, as the conditions of the case determine.

Secondly, what do we mean by intensity and by direction of light? Are we justified in assuming that a stimulus such as light can be effective in causing either kind of orientation through its directive quality? The answer to these questions depends largely upon arbitrary definitions. YERKES' (1903) exposition of what constitutes a phototactic reaction as differentiated from a photopathic reaction indicates very nearly the meaning that will be given to these terms in the present paper. Attention may be

called to one difference, however. It is inferred by YERKES that the sign of the phototactic response is dependent upon the previously assumed body-orientation of the organism. This is by no means necessarily true, for in the case of the larval lobster, it is clear that the orientation of the body has absolutely nothing to do with the sign of the consequent progressive orientation. For our present purposes we may, therefore, slightly modify the definition of YERKES by describing a *phototactic reaction as one in which the organism tends to place the longitudinal axis of the body parallel to the direction of the rays and to approach or recede from the source of those rays.*

If we so limit the meaning of a phototactic response, what shall we say regarding the nature of the so-called photopathic response? It is entirely possible (and indeed in the case of the larval lobsters, most probable) that again the view of YERKES (1903), that a photopathic reaction is one in which an organism "selects" a particular intensity of light, and confines its movements to the region illuminated by that intensity, is correct. But it is not so certain that the photopathic responses of the lobster larvæ are brought about by means of slight phototactic reactions, as YERKES (1903, p. 1) suggests for *Daphnia*. Therefore, for present needs, we may conclude that a *photopathic reaction is one in which an organism, without previous assumption of a body-orientation, "selects" regions of optimal light-intensity.* In the following account of experiments and observations, we shall see to what extent the behavior of the lobster larvæ conforms to these definitions of phototactic and photopathic reactions.

The movements of Entomostraca toward or from a source of light, and their reactions to rays of different wave lengths have been made the subject of investigation by many naturalists. In the earlier investigations it was commonly concluded that the intensity of light was the most important factor, and that organisms "chose" an optimal intensity. LUBBOCK (1881) and GRABER (1884) found that *Daphnia* gather in areas of greater light intensity. SCHOUTEDEN (1902) found that older individuals are negatively phototropic. These experiments, as repeated by DAVENPORT and CANNON (1897), YERKES (1899, 1903), and PARKER (1902), showed that *Daphnia* also manifests phototactic reaction. It was assumed, therefore, that some organisms may react either phototactically or photopathically. Later work of American in-

investigators has demonstrated that the Crustacea are more influenced by the directive factor of the light rays than by the intensity, and, more recently still, KEEBLE and GAMBLE (1904), in their excellent work on the color physiology of the higher Crustacea, have shown that the nature of the background may be an important factor in determining the reaction of many species.

The Malacostraca have received less attention than have the Entomostraca, and it is only for a comparatively short time that anything has been known concerning the reactions of either the larvæ or the adults of decapod Crustacea. With the adult forms of the decapods results have been readily obtained. HOLMES (1901) found that several species of terrestrial amphipods manifest a strong positive phototactic reaction, while all aquatic species are negatively phototactic. We know further from KEEBLE and GAMBLE (1904) that the adult form of *Palemon* is negatively phototropic and that *Hippolyte* is positively phototropic. *Hippolyte*, according to KEEBLE and GAMBLE, not only moves toward the light, but also "prefers" a white to a black background. *Macromysis inermis* reacts positively or negatively in accordance with the character of the background or the nature of the physical environment. It is positively phototropic on a white background, and negatively phototropic on a black background. Furthermore, when a choice of background is made possible, *Macromysis* "selects" the black. In the case of *Hippolyte*, the larvæ respond positively to light, as do the adults. BELL (1906) states that the adult crayfish is "somewhat negatively phototactic" and that difference in the intensity of light made but slight difference in the reactions. Other investigators have shown that the adults of several species of Crustacea react either positively or negatively to light. Very few investigators, however, have studied systematically the reactions of Crustacea in the larval stages. Among the first, LOEB (1893) reported the reactions to light of *Limulus* in the "trilobite stage." These larvæ, he said, are at first positive, and later, negative. PEARL (1904), by repeating LOEB's experiments, ascertained that this larval stage of *Limulus* manifests at first a negative reaction, and that later, a relatively small number of individuals gives a positive reaction. It was learned by KEEBLE and GAMBLE (loc. cit.) that the response of the larvæ of *Palemon* is the direct opposite of the reaction of the adults. BOHN (1905) discovered that the larvæ of the European lobster (*Homarus vul-*

garis), although at first positive in their reaction to light, may later undergo certain changes. HERRICK (1896) states that larvæ of the American lobster react positively to light. BOHN (1905) learned that the reaction of *Artemia salina* was similar to that of *Homarus vulgaris*; and the writer has ascertained that the larvæ of the green crab, *Carcinus granulatus*, react sometimes positively and sometimes negatively, and behave very much like the larvæ of the lobster. The writer can verify the conclusions published by LYON (1906) that the larvæ of *Palemon* may react either positively or negatively to light.

The results of the small number of investigations which have been made upon the reactions of Crustacea in the larval stages, indicate the desirability of further systematic study of these reactions. PEARL (1904) has well pointed out the value of studying the "ontogeny of reaction," and of applying the knowledge thereby gained to the investigation of the more complex forms of response exhibited by adult individuals. Although the writer has not yet had an opportunity to study the behavior of the adult lobster, the present work shows that in the larval stages there are found diverse types of reaction, differing from one moment to another, and depending upon conditions which, even in the nicest experiments, are by no means readily discoverable; and, furthermore, that it is only by a systematic study of the reactions *through the developmental stages*, that many contradictory points can be cleared up, and the more complex behavior of the older animals explained.

II. BIOLOGY OF THE LOBSTER.

A brief résumé of the biology of the lobster will facilitate the understanding of later considerations. The life of the lobster consists of a series of stages or stage-periods, each of which represents the span of life between two successive moults, or castings of its shell. Of these stage-periods, the first four are passed through very rapidly, since the young creature usually moults four times in the first twenty days of its existence. These first few quickly passed stages (called the larval stages because they denote the successive emergence of one from another) include the most important changes in form, color, and manner of behavior, that the lobster undergoes. In each successive stage the animal is larger than before. The larvæ grow at the time of

moulting, but never between moults. From the fourth stage on, each successive stage-period is of longer duration and the changes which the adolescent lobster thenceforth undergoes are correspondingly less significant, being characterized chiefly by alterations in internal morphology as the adult functional type is gradually approximated. The first three stages of the lobster are free-swimming stages, and the activities are without apparent

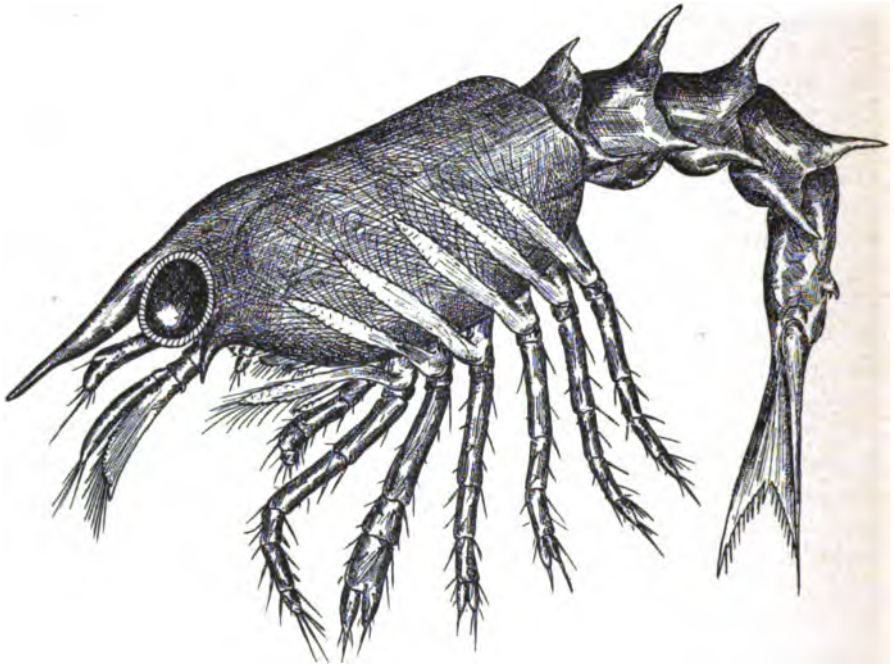


FIG. 1. Showing a young first-stage larval lobster about two days old. The eyes are large and prominent. The exopodites of the thoracic appendages are represented at the beginning of the downward stroke. This figure shows the typical swimming position of larvæ in the first three stages, the plane of the cephalo-thorax bent down at an angle of about 30° from horizontal.

coördination or aim. The larvæ are swept here and there by the tide and possess no power to evade the attacks of numerous enemies.

The swimming of the lobsters of the first three stages is accomplished by means of the feathered exopodites, or outer branches of the thoracic appendages (Fig. 1). These exopodites beat the water with short vibratory strokes, which tend to carry the larva back-

ward or forward or upward as the case may be,² and allowing it to sink toward the bottom when their motion ceases. The progressive movement and the body-orientation of the lobster in the first three stages are almost wholly dependent upon the activity of these organs. Occasionally, darting backward movements, caused by the sudden contraction of the abdomen, appear, but these are of slight importance in the reaction to light.

When the lobster moults to the fourth stage, the exopodites are lost. Consequently the forward swimming during and after the fourth stage is dependent upon the action of swimming appendages which after the second stage make their appearance on the under sides of the second, third, fourth and fifth abdominal segments. The fourth-stage lobsters swim with directness and precision, usually near the surface of the water. This surface-swimming may be due to stimulation by light, but, as the writer has suggested elsewhere (1906b), it is not improbable that this form of behavior is due in part to the food-seeking impulse. During the latter part of the fourth stage, contact-irritability begins to play an important rôle in determining the behavior of the young lobster. Now, as in the fifth and later stages, the creature no longer swims at the surface of the water, but seeks the bottom and attempts to burrow in the sand or beneath any object that presents itself. After the fifth stage, the adolescent lobster shows the same type of behavior as during the fifth stage, but with a gradual increase in the tendency to avoid light. Its reactions have now become fixed in every way.

III. APPARATUS AND METHOD OF PROCEDURE.

The manipulation of the various pieces of apparatus here described will be spoken of when the particular experiments in which they are used are mentioned. The room in which the experiments were conducted contained on two of the opposite walls windows 2 feet high and 8 feet long, before which extended work benches or tables. The two windows, which opened respectively to the east and west, were the only source of daylight, and, as occasion required, were heavily screened with black paper or cloth. At appropriate places in these screens were cut openings which could be readily closed. On the table before one of the windows was

² For details on method of swimming, see p. 258.

placed a box 2 feet high, 3 feet wide, and 2 feet deep, lined on the inside with black cloth, and containing, on the window side, slits or openings to correspond with the openings in the screen outside the box. On the room side, the box was fitted with a movable black curtain, which permitted the operator to move the jars or other apparatus contained within the box. This arrangement served to control the light falling upon the larvæ, which were put in suitable containers and placed inside the box.

Other pieces of apparatus may be described as follows: *Glass box A.* Of glass boxes two types were used for studying the photopathic and phototactic reactions of the larvæ. One was a rectangular wooden box having glass "windows" in each end and in the bottom. This box, which was 12 inches long, 6 inches wide, and 3 inches deep, was painted dull black on the inside and fitted with a light-tight cover. It was used in experiments which required illumination from the end, from below, or both.

Glass box B—This box was similar in most respects to box *A* (see Fig. 7). It was 12 inches long, 6 inches wide, and 5 inches deep. It had "windows" on each end and along one side. Like box *A*, it was painted black on the inside and was fitted with a light-tight cover. This cover contained three slits so arranged that diaphragms of wood or glass might, in an instant, be slid into place to divide the box transversely into four chambers of equal extent. Then the cover of the box might be removed if desired, leaving the partitions in place. The object of this arrangement was to make it possible to imprison the young lobsters wherever they chanced to be at any given time and so to ascertain, by count, in what manner and in what relative numbers they had responded to certain stimuli.

Of these two boxes, the former, while oftener placed in a level position on a laboratory table, was sometimes used in another way to study the photopathic reaction alone, or the photopathic and the phototactic reactions together. In these cases the box was placed over a light-shaft, which was merely a rectangular tube lined with black cloth, with a height of 18 inches and with a cross section of the same size as the bottom of the box. Over the upper end of this tube or shaft, the glass bottom of box *A* exactly fitted. At the bottom of the shaft was either a sheet of white paper or a mirror which was so placed as to reflect the rays of light coming from the window up through the shaft to the glass bottom of the

over-lying box. The rays that thus passed through the black-lined shaft and entered the box were practically parallel and at right angles to the plane of the bottom of the box. It is clear that, when the water in the box was very shallow, the rays of light passing up the shaft and striking the larvæ could have no directive influence, and that, when they passed through the graded light screens or through plates of colored glass, placed just beneath the glass bottom of the box, they could be effective only through difference in intensity.

Besides these boxes, use was made of certain glass jars, known as museum or brain jars, which were for the most part cylindrical in shape and varied in diameter from 20 to 25 centimeters. For certain experiments these were covered wholly or partially about their circumference with black paper, and the light was made to come from the top, bottom, or through a "window" in the side, as the case might require.

In addition to the apparatus mentioned above, several kinds of glass tubes were employed. Some were ordinary 15 centimeter laboratory test tubes, while others had a length of 40 centimeters and a diameter of 4 centimeters. These tubes were made with rounded ends so that there would be no obstruction to the light striking the tubes even at a slight angle, and the lobsters were introduced through an opening in the top. Another type of tube employed was the Y-tube, constructed of glass tubing, 4 centimeters in diameter as shown in Fig. 5. These proved exceedingly useful in testing the reactions of young lobsters, both to the intensity and the directive influence of the light rays, since the arms of the Y-tube could be readily covered with colored glass plates or fitted with black or white backgrounds, thus producing different conditions of light in each arm of the Y.

In many of the experiments it was desirable to use graded light screens. These were made by adding india ink to a solution of gelatine and allowing this to harden in the form of a wedge. The wedge-shaped screen permitted light to pass through in diminishing amount, from the thin edge to the thick edge, which was quite opaque. Graded light screens of red and blue were also made by adding to the gelatine a solution of eosin or methylene blue. It was by means of these, together with the colored glass plates that differences in the intensity of light were secured.

Since a particular response to light is often interpretable only

when the conditions previous to the hour of experimentation are taken into account, it was found desirable to secure such conditions for experiment that all influences which might be instrumental in determining the final reaction of the larvæ either before or during the time of actual experimentation should be clearly recognized. Accordingly, the data to be presented show not only the nature of the reaction of the larval lobsters at a few chosen periods in their life history, but they also make it possible to trace modifications in reaction as the young animals pass on from stage to stage and gradually approach the adult type. Numerical results were usually obtained by counting the larvæ which had been imprisoned in different compartments of the box by the sliding partitions. In other cases a large number of larvæ were put into a glass jar and the reaction of the majority was observed. The separation and selection of larvæ which gave either a positive or a negative reaction to the same stimulus was thus possible, but conclusions have been drawn only after a careful study of the exact accounts of many groups of larvæ. The exact intensity of light used in the experiments was not known, but the experiments were performed on such days and at such times as would make the conditions uniform. Before entering upon a detailed consideration of the experiments as a whole, it will be appropriate to state some ground for assuming that lobster larvæ react both to the intensity and to the directive influence of light. The preliminary experiments which led to this view may be presented as follows:

IV. PRELIMINARY EXPERIMENTS.

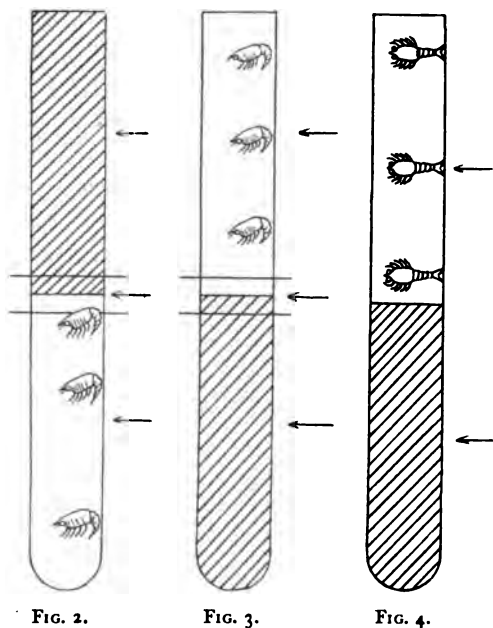
Experiment I—Glass tubes 15 centimeters long and 2 centimeters in diameter were filled with salt water and in each were placed six first-stage lobsters two days old. When the tubes were held vertically, there was no tendency shown for the larvæ to gather in any particular region of the tubes. When, however, a strip of black paper was wound in such a manner as to cover the upper half of a tube (Fig. 2) and records were taken every minute, the larvæ became distributed as follows:

NUMBER OF LARVÆ PRESENT AFTER	UNSHADED AREA.	AREA WHERE LIGHT AND DARK MEET.	SHADED AREA.
1 minute.....	5	1	0
2 minutes.....	6	0	0
3 minutes.....	6	0	0
4 minutes.....	6	0	0
5 minutes.....	5	1	0
Total.....	28	2	0

It will be seen that the larvæ "seek" the light area. Next the paper was so arranged that the shaded part was below, as shown in Fig. 3. In this case the larvæ were always found uniformly in the unshaded area. In all cases the body-orientation of the larvæ was determined by the direction of the rays of light, which struck the tube at right angles; but at no time, it would seem, could this directive influence alone have been instrumental in causing the larvæ to remain in the region of greater light-intensity. The same general results were obtained when the tubes were laid horizontally on the table (Fig. 4) but still at right angles to the direction of the incident light rays which came from the side. These tests of the reaction of larvæ in glass tubes appeared at first sight to demonstrate that larvæ of a certain age and stage show a tendency to group themselves in regions of greater illumination, irrespective of the directive influence of light or of reaction to gravity. This, however, is not the only possible conclusion to be drawn from these facts.

To take, for instance, the case of the horizontally lying tube (Fig. 4), in which the larvæ gathered in the illuminated ends (the region of greatest light-intensity), and there oriented to the directive influence of the light. In the darkened area of the tube the larvæ did not undergo body-orientation, but swam about in many directions. When occasionally, they entered the more brightly illuminated end of the tube, they at once oriented to the directive influence of the rays and took the position shown in Fig. 4. Furthermore, the larvæ usually manifested a tendency to retain their body-orientation and thus to remain in the illuminated region when once they had entered it. Here, then, we have a case where the apparent reaction to the intensity of light is, in reality, determined, and maintained, partly at least, by the orienting response to the directive influence of light. In other words, the larvæ did

not, in this instance, "select" the region of greater light-intensity because of the intensity *per se*, but because they became imprisoned in it through orientation as a result of the directive stimulus. It is only through rays which strike the larvæ directly from above or from below that an approximately non-directive influence can be obtained.



FIGS. 2 and 3 show the orientation of the larvæ in tubes standing in the vertical position; Fig. 4, in the horizontal. The arrows represent the direction of the light rays striking the tubes from the side. The cross hatching represents the parts of the tubes covered with black paper.

Experiment 2. Reaction to intensity of light—In this experiment use was made of the glass-bottomed box *A* with the light-shaft, and the colored-glass plates or graded light screens. First the glass plates were arranged over the top of the light-shaft in the order blue, green, orange, red. The box was filled with salt water to a depth of 15 mm., and ten first-stage larvæ were placed therein. The light-tight cover was then put in place and the larvæ were allowed five or more minutes to become acquainted with their new environment. The result was as follows:

TIME.	BLUE.	GREEN.	ORANGE.	RED.
After 5 minutes.....	10	0	0	0
After 10 minutes.....	10	0	0	0
After 14 minutes.....	9	1	0	0
After 17 minutes.....	9	0	0	1
After 19 minutes.....	9	0	1	0
Totals.....	47	1	1	1

The results of these tests and others in which the order of the glass plates was changed, demonstrate the tendency of the larvæ to group themselves in the blue, which was the more brightly illuminated region. Similar experiments were performed with graded light-screens (strips of paper of different thickness or a gelatine wedge) substituted for the glass plates. The results in every case indicated that here also the larvæ reacted to difference in intensity. These experiments were performed with a belief that it is the refrangible rays of the spectrum alone that are active in determining the phototropic reactions of animals and plants. MIN-KIEWICZ (1906), however, has found that, although positively heliotropic animals usually react positively to the rays of shortest wave-length (violet or blue), and negatively heliotropic animals usually react to the rays of greatest wave-length (red or yellow), these phenomena of positive phototropism and positive chromotropism are not necessarily found together in the same organism. It is uncertain whether or not the larvæ of *Homarus* manifest chromotaxis. At the present time it can be said that the observed reactions of the larvæ to colored lights agree so well with the reactions to lights of varying intensity as determined by light screens, that they may fairly be considered responses to difference in intensity of light.

Experiment 3. Reaction to the directive influence of the rays—To demonstrate the response of the larvæ to the directive influence of the light rays the description of a single experiment will suffice. Similar experiments will be recorded later, in another connection. The conditions of this experiment are like those described in Experiment 2, i. e., box *A* was mounted over the light-shaft on the colored glass plates arranged in the order blue, green, orange, red. The ten first-stage larvæ contained in the box were more or less constantly oriented in the region of greatest light intensity, that is over the blue glass. Next, the small window situated at

the red extremity of the box was opened to the diffuse light of the room. The result was that the larvæ immediately oriented to the new rays, left the region of greatest light-intensity, the blue area, and moved backward in the direction of the incident light rays toward the source of the weaker light and, at the same time, into a region of lesser light-intensity at the red end of the box.³ The distribution at the end of 19 minutes was as follows: blue, 4 individuals; green, 1; orange, 1; red, 24. Here it appears that the larvæ, which at the beginning of the experiment were grouped in the area of greatest illumination under the influence of non-directive rays, were forced by the directive influence of the new rays to move from a region of greater into one of diminished light-intensity. As will be observed later, this experiment was tried under a great variety of conditions, and with larvæ of different stages and ages, with uniform results. Whenever the larvæ had an opportunity to move in the direction of the rays, they would do so, notwithstanding the fact that they thus passed from a region of greater to one of less illumination.

In the paragraphs immediately preceding, the purpose has been merely to indicate that in the behavior of the lobster larvæ we may observe reactions both to the intensity of light and to the directive influence of the light rays. The latter depends, first, upon the unequal stimulation of the two eyes, and second, upon the degree of illumination which affects both eyes. The conclusions which have been drawn from these few experiments receive further support from other experiments. But first, it is necessary to know whether there is any form of reaction common to all larval lobsters. To answer this question, which is of primary importance, it will be necessary to report in detail a series of tests, which were made upon many groups of lobsters during different periods of their metamorphosis and under different conditions of stimulation by light.

Experiment 4. Case 1—In several instances larvæ which had been hatched from one-half hour to one hour were put in a glass jar, which was in turn placed in the dark box and submitted to illumination on one side from a narrow window. In every case

³ If this experiment appears uncritical because of the lack of information regarding the exact intensities of light at the opposite ends of the box, it may be answered that the intensity of light was measured by the only method available. Sensitized paper was placed inside the box, one strip over the end window, the other over the bottom at the blue end. The results showed that the light entering the blue end through the bottom of the box was much stronger than that entering the end window from the room.

the young larvæ at once swam backwards toward the source of light and grouped themselves closely together at the window side of the glass jar. So perfect was this orientation on the part of the newly hatched larvæ that, out of 100 individuals, not one showed a negative reaction.

Case 2—When the same larvæ were put in one of the long 40-centimeter glass tubes so placed in the dark box that the tube was parallel to the direction of the incident rays, the young lobsters in every case swam rapidly to the end of the tube nearest the window and remained there until the tube was reversed, when they again swam toward the window. These reversals might be continued for hours.

Case 3—When the same individuals, or other larvæ of the same group, were placed in box *B*, and this was turned with one end toward the window, the reaction of Case 2 occurred. They swam backward toward the window.

Case 4—Another group of fifty first-stage larvæ three days old was placed in a glass jar in the dark box and illuminated from the small window. All were definitely positive. Next, the circumference of the jar, except a vertical strip three inches wide on the light side, was covered with black paper, and the jar was so placed that direct sunlight had access to the open side. The larvæ immediately gathered on the darker side of the jar and remained there for one and a half minutes, after which they again returned to the sunlit side and remained there in bright sunlight as long as they were observed.

Experiment 6.—July 19, 3:30 p.m. Fifty first-stage larvæ, two days old, were put in a glass jar and this was placed in the dark box. Though the light was not bright at this time in the afternoon all the larvæ gave a positive reaction. The jar now was placed on a black background in the bright sunlight on the west table. Every lobster moved to the room side of the dish away from the light. Within two minutes, many began to go back to the window side, and this continued until all were again gathered there. After four minutes, however, they again returned to the room side and remained there for ten minutes, at the expiration of which time they were about equally divided between the room side and the window side of the jar. They were now put back in the dark box, and with the slight intensity of light at 7 o'clock in the evening, all were reacting positively. By 8:30 the box was fairly dark and the

orientation of the larvæ was indefinite. Suddenly the rays of a powerful acetylene light were thrown upon the jar. Immediately a negative reaction took place and continued for two minutes, when some of the larvæ began to return to the light. At the expiration of four minutes all the larvæ were reacting positively, and this reaction continued for several hours.

Experiment 7—July 22, 9:30 a.m. Forty-four second-stage lobsters, six days old, were placed in the glass jar, in the dark box. Eleven came at once to the room side of the jar. The jar now was moved nearer the small (three by three inch) window. As a result seventeen out of forty-four individuals gathered on the room side, but the definiteness of the positive reaction on the part of the window-side lobsters was lessened by desultory swimming. The jar was next placed on the west table, the room side and top of the jar being shielded by black paper. All the larvæ came to the room side of the jar. When replaced in the dark box (in light of much lesser intensity), the reaction again became uniformly positive.

Experiment 8—July 23, 9 a.m. Forty second-stage larvæ, seven days old, were placed in the glass jar on the east table, and exposed to strong light. All the larvæ at once oriented on the room (darker) side of the jar. These lobsters were next placed on the west table where the negative reaction continued throughout the afternoon. From 6 to 8 o'clock in the evening the light faded gradually. At 7:35 the body-orientation was nearly lost, but the orientation on the room side of the jar with diminishing definiteness remained in effect until 7:50, when the light had faded quite away and the lobsters were scattered throughout the jar.

Experiment 9—July 28, 9:30 a.m. Twenty third-stage lobsters, twelve days old, were placed in the glass jar in the dark box on a white background and submitted to light of slight intensity coming through the small window. All showed a strong positive reaction, and gathered on the window side of the jar. The next day in the afternoon, about fifty third-stage larvæ of the same group, now thirteen days old, were placed in the glass jar in the dark box on white background and submitted to light of medium intensity. Nearly all of the larvæ oriented on the room side of the jar, thus demonstrating a definite negative reaction.

Experiment 10. Case 1—June 26, 9 a.m. Ten fourth-stage lobsters, fifteen days old, were placed in the glass jar in the dark box

and submitted to light of medium intensity from the small window. There was no appreciable tendency to undergo either body or progressive orientation. The lobsters were much engaged in eating one another.

Case 2—The fourth-stage lobsters mentioned in the preceding paragraph were fed on chopped clam meat and placed in box *A* with the black interior. Light was admitted through the end window. Records of four tests made at two-minute intervals show that while nine were neutral in reaction, six were positive, and twenty-five were negative. The box was next lined with white paper and the same fourth-stage lobsters were submitted to the same external light conditions. The results show twenty-six positive, twelve neutral, and twelve negative individuals.

Case 3—August 7, 2:30 p.m. When twenty fifth-stage lobsters, twenty-five days old, were put in box *A* and illuminated through the end window, all, without exception, oriented in the dark end of the box.

Conclusions concerning the permanence of these reactions through the stages—In explanation of the ten experiments recorded above, it should be stated that the writer had at his command large numbers of larval lobsters of approximately the same age and stage which had been subjected throughout the whole of their early life to the same conditions of environment. Therefore it was possible to make a detailed systematic study, not of a few isolated individuals alone, but of whole groups. The result of this study is expressed in these experiments.

Whatever else the foregoing facts may demonstrate, the answer to our first question is evident. *There is no constant form of reaction on the part of the larval lobsters to the directive influence of the light rays.* For this reason one has no warrant for saying, without reservation, that the larval lobster is either positively or negatively phototactic. If it had been necessary to depend for material upon a few individuals of uncertain age, and to draw conclusions regarding the general behavior of all the larvæ after observing the behavior of these few individuals, the outcome would of course be far less satisfactory than in the present instance. It is to be regretted, perhaps, that no means were at hand to make a critical determination of the exact intensities of light to which the larval lobsters gave their recorded reactions, but it is apparent that such a refinement of method would not change the general conclusions reached.

With the foregoing facts in mind, it is clear that the problem before us becomes, not, what reactions do the larval lobsters in general give to light, but *how do the lobster larvæ of a certain age react to light under certain known conditions?* To this rather more complex question attention will now be given.

V. SYSTEMATIC ACCOUNT OF THE REACTIONS TO LIGHT OF LOBSTERS IN THE LARVAL STAGES.

What is the nature of the reactions to light through the successive developmental stages, and by what conditions is it determined? Regarding the first of these points, it should be borne in mind that the subject matter concerned cannot be treated concretely, but that it is necessarily scattered through the long series of observations which follows, and that it is only from a consideration of the series *as a whole* that a clear idea of the gradual modifications in the reactions from the first to the sixth stage of the lobster's life can be obtained. As to the second point of inquiry, it is at once perceived that the conditions or factors which we seek to discover are of two sorts:

1. *Conditions which are peculiar to a certain definite age or stage in the development of the larva, and which may be designated as physiological conditions.*

2. *All outside influences, including the intensity and multiplicity of stimuli brought to bear upon the animals.*

In the following discussion it will be found of advantage to consider these two kinds of modifying conditions together; for they are found to be very much inter-related when a consideration of their mutual importance in bringing about any orientation of the young lobsters is involved.

It may be appropriate to mention at this point the method of securing the data here presented. The futility of taking young larvæ at random from the hatching bags without knowledge of their age or previous history was recognized early in the course of the investigation. It was considered advisable to work only with those lobsters whose previous history was definitely known. To this end the exact time of hatching of certain groups of larvæ was noted. In the large canvas hatching bags, used at the Wickford Station, hundreds of larvæ hatch in a single hour, and observations were made, as a rule, twice each day (morning and afternoon), upon

individuals taken from these groups, whose age was accurately known. During the course of the study, the history and the daily reactions of three groups of larvæ were followed and recorded. For the following account of the reactions of the first-stage larvæ, for instance, the records of these three groups for the first day, the second day, the third day, etc., were used. Only the reactions which appeared to be the most constant and typical have been introduced here. Therefore, although many variations in reactions were found to occur, the following section describes the typical daily reactions of the larval lobsters from the time of hatching through the fifth stage of their existence.

1. First Larval Stage.

As has been shown by preliminary observations and the experiments already mentioned, the lobsters of the first larval stage are usually strongly positive both in their photopathic and in their phototactic reactions. These reactions are manifested strongly in the few hours directly after hatching, when, as we shall presently see, the young lobsters react definitely, and to very slight differences in the intensity of illumination. When half-hour old lobsters were placed in the glass jar, and submitted to any kind or intensity of light (daylight, artificial, or colored), they responded well (especially when the intensity was increased by a white background) to slight differences in illumination; and reacted uniformly and invariably by moving, tail foremost, toward the source of light. In case of two sources of light, on opposite sides of the jar, the larvæ would respond to the rays which were the more intense. If the rays from two sources of light were introduced at right angles to each other, the resultant reaction, as has been shown for other organisms by many investigators, was determined according to the law of the parallelogram of forces.

It would appear that, in the behavior of the first-stage larvæ, we have the most delicate reactions to slight differences in light intensity that occur throughout the life of the lobster. During the early hours of the first larval stage, no individuals reacted negatively to the directive stimulus of the light, while in the later stages, although a majority of the larvæ manifested definitely one reaction or another, there were usually a few individuals which gave responses that were either indefinite or opposite to the rule.

Experiment 11. Case 1—Ten first-stage larvæ, five hours old, were placed in a glass tube 40 cm. long, and this was laid on the table at right angles to the plane of the window and parallel to the light rays entering through a narrow slit in the screen. All of the larvæ at once oriented themselves at the window end of the tube. Next, blue, green, and yellow glass plates were placed successively over the end of the tube next the window, leaving the opposite end clear, but none of these changed the definiteness of the positive reaction. When, however, an orange glass was used, the larvæ paused midway in the tube, at the border line of the orange light, and in their final orientation were scattered between this region and the orange end of the tube. When a red glass was superimposed, all the larvæ took a position at the border line of the red and the clear glass, this region representing the junction of the areas of strong and weak illumination.

Experiment 12. Case 1—In this experiment the glass bottomed box *A* was set up over the light-shaft with the colored glass plates arranged in the order, red, orange, green, blue, as described on p. 207. The box was filled to a depth of one inch with water and first-stage larvæ, twenty-four hours old, were introduced. Five minutes was allowed for the larvæ to become acquainted with the new environment. Records of four tests then made showed that while thirty-eight larvæ gathered in the blue area, only one was found in the red, one in the orange, and none in the green. Changing the order of the glasses in no way changed the results. This apparently demonstrates that there is a definite tendency on the part of these larvæ to orient themselves over the glass plates which admit the brightest light; and that the precise order of the plates makes no difference in orientation.

Case 2—In this instance the order of the glass plates was red, orange, green, blue. The same larvæ used in the above tests were employed, but the conditions of the experiment were changed. The window in the end of the box corresponding to the red glass was uncovered and the diffuse light from the room was allowed to stream through the box longitudinally. The object of this was to discover whether the larvæ which had previously given so definitely the positive photopathic reaction, could be induced to enter the region of diminished light intensity (at the red end of the box). In other words, whether the phototactic reaction could be made to overcome the photopathic. Between each of the successive

tests mentioned below, the light from the room and the light through the shaft were cut off in order that a scattering of the larvæ through the box might occur. In other cases the position of the box was reversed; and in still others both the position of the box and the order of glass slides, changed. The results of four tests are as follows (the arrow represents the direction of the light entering the end window of the box):

TEST.	AFTER	DISTRIBUTION OF LARVÆ.			
		→ Red.	Orange.	Green.	Blue.
1	45 minutes	8	0	0	2
2	9 minutes	8	0	0	2
3	14 minutes	8	1	0	1
4	18 minutes	9	0	1	0
Totals		33	1	1	5

Case 3—In this instance the red and orange glass plates were removed and black paper substituted. The photopathic reaction was found to be definitely positive, the young larvæ grouping in the blue area. Now, as before, the window at the end of the box corresponding to that overlying the black paper was opened to the subdued light of the room, while brilliant daylight entered the blue end of the box. As will be observed, the conditions of this experiment are similar to those of Experiment 11, save that, in this instance, a greater difference between the intensity of light at opposite ends of the box existed. Between tests the light from both sources was cut off and the larvæ were allowed to scatter. The results, which may receive the same interpretation as those of Experiment 11, are tabulated below (the arrow indicates the direction of light entering the end window of the box):

TEST.	AFTER	DISTRIBUTION OF LARVÆ.		
		→ Black.	Green.	Blue.
1	5 minutes	10	0	0
2	7 minutes	7	3	0
3	10 minutes	10	0	0
Totals.....		27	3	0

Conclusions from Experiments 11 and 12: In the results of the foregoing experiments, we have further evidence to support the conclusions drawn from Experiment 3. In Experiment 12 the larvæ passed from a region of greater (blue) to one of lesser (the red, or in Case 3, the black) light-intensity in moving toward the source of light in the direction of the incident rays. It must be assumed that in Case 3, there was a much greater difference in the intensity of light at the two ends of the box (overlying the blue glass and the black paper respectively) than in Case 2, or in Experiment 3. These experiments were performed many times, under several different conditions of light, and with larvæ of ages varying from a few hours to two days. The same results were obtained in every case, except that in the older first-stage larvæ the reactions were not so definite (more individual variations) and a stronger light was required to bring about the same responses as were manifested by larvæ under four hours old. In these cases, as also in Experiment 3, rays of lesser intensity (but in a horizontal plane) which struck the larvæ in such a way as to cause a body-orientation in which a normal swimming position was still maintained, were more influential in determining a progressive orientation than were the more intense rays which struck both eyes equally, but which came from below, and had a tendency (as will be shown in detail later) to throw the larvæ out of their normal swimming position. As the writer has shown elsewhere (1907a), galvanotactic reactions in the young lobsters occurred only when the tail or the back was turned wholly or partly toward the anode. Although at first sight it appears that the causes for this condition of reaction can have nothing in common with the causes which determine a progressive orientation to the directive influence of light rays only when the swimming position is favorable, it may not be inappropriate to suggest that here also the direction of the impact of light with reference to the axis of the body of the larva, may have some influence on the reaction.

Experiment 13. Case 1—Ten larvæ, twelve days old, were placed in box *A*, mounted over the light-shaft. When the glass plates were arranged in the order designated below, the photopathic reaction was as follows:

TEST.	AFTER	DISTRIBUTION OF LARVAE.			
		Red.	Orange.	Green.	Blue.
1	5 minutes	0	1	2	7
2	10 minutes	1	1	1	7
3	15 minutes	1	1	2	6
4	20 minutes	2	0	0	8
5	25 minutes	0	1	0	9
Totals.....		4	4	5	37

Case 2—When the order of the glass plates was changed to red, blue, orange, green, the following results were obtained: Red, 3; blue, 31; orange, 3; green, 3.

Case 3—After redistribution of the larvæ had taken place, the small window opening at the green end of the box was uncovered to the diffuse light of the room. The resulting reactions were as follows:

TEST.	AFTER	DISTRIBUTION OF LARVAE.			
		Red.	Blue.	Orange.	Green.
4	2 minutes	0	3	3	4
2	4 minutes	1	3	3	3
3	7 minutes	1	3	1	5
4	10 minutes	1	2	3	4
Totals		3	11	10	16

Case 4—Once more the order of the glass plates was changed to blue, green, orange, red, and the window at the red end was uncovered to the light of the room. The results of the three sets of tests were: Blue, 9; green, 5; orange, 3; red, 13.

Experiment 14—The following observations deal with cases of larvæ suddenly submitted to a light of great intensity, as for instance when they are brought from subdued daylight into full sunlight, or when the brilliant rays from an acetylene lamp fall upon larvæ which had been for sometime in darkness.

Case 1—July 18, 4 p.m. Fifty first-stage larvæ, about thirty hours old, which had been reacting positively in lights of low or medium intensity, were placed (in a glass jar) in the bright sunlight of the west table. Every larva at once moved to the room side of the jar. Within a few minutes, however, all returned to the window side of the jar. Ten minutes later they were divided

about equally on each side. Next they were returned to the dark box and submitted to the weak light from the small window. Here they manifested a definite positive reaction which continued until evening. At 8:30 these fifty larvæ were suddenly submitted to the intense rays of an acetylene light. The result was a universal negative reaction. Within two or three minutes, however, a few larvæ began to return toward the light, and within four minutes all had become positive in their reaction.

Case 2—A group of fourth-day first-stage larvæ in the glass jar was subjected to light of low intensity and found to manifest a positive reaction; when subjected to a much stronger light the same larvæ were still universally positive. This reaction, once established, endured through the period of gradually diminishing intensity of light accompanying the coming of night. The next morning these (now fifth-day) larvæ were found to be negative in reaction. It was feared, however, that the manner of reaction might have been changed because of the long period of confinement which they had undergone. For this reason a fresh lot of twenty-five larvæ from the same group (fifth-day, of the first and second stages), was secured. It was observed at this time that about a third of the number of those in the hatching bag had moulted into the second stage, and that the others were very near the moulting-period. When these larvæ were put in the glass jar, placed in the dark box and submitted to subdued light from the small window, six tests showed fifty-five to be negative, and ninety-five positive. When these same larvæ (now thirteen first-stage and twelve second-stage), under the conditions of stimulation stated above, were subjected to light of still greater intensity by placing the jar nearer the small window of the dark box the results showed that fifty-nine were negative and forty-one were positive.

At 3:30 p.m. these same larvæ were removed from the dark box and placed (in the glass jar) on the west table, where they were suddenly subjected to the bright afternoon sunlight. Every larva came to the room side of the jar and remained there so long as observed.

Case 3—The larvæ mentioned above were liberated and another lot of twenty-five (of the same group, but all in the second stage) was secured at 8 o'clock in the evening. The intense rays of the acetylene light were suddenly directed upon one side of the jar.

This resulted in a sudden and universal positive reaction which, however, soon became indefinite. The larvæ gradually returned to the darker side of the jar and, as in the case mentioned above, remained there so long as observed.

Case 4—When, on the other hand, another group of larvæ which was reacting positively to a light of low intensity, was brought by slow degrees into a light of great intensity, there resulted no sudden, temporary change of reaction such as that observed above. The reaction usually remained unmodified, but if it was reversed it remained permanently so. The same statement holds for larvæ which had been reacting negatively to light of low intensity. When they were brought by slow degrees into light of great intensity, seldom did a sudden temporary change in reaction result.

Conclusions from Experiment 14: The stimulation brought about by suddenly submitting larvæ to intense light may cause at least two kinds of response: first, in the case of early first-stage lobsters (about thirty hours old, and manifesting previously a positive reaction), a definite and universal, though temporary, negative response; second, in the case of early second-stage larvæ (about five days old, and giving previously a negative reaction), a definite and universal, though temporary, positive response. From Case 4 it appears that a gradual change of intensity (extending over an equal or even a greater range of intensities) may not bring about a similar result, although a permanent reversion in the reaction may sometimes ensue.

Larvæ which have recently moulted are most susceptible to slight differences in light-intensity; and the reaction of such larvæ is frequently negative, while the reaction of larvæ which are approaching the moulting-period is more often indefinite or positive.

Experiment 15. Case 1—The following experiment involved the use of the Y-tubes described on p. 207. Ten positively reacting lobsters, five hours old, were placed in the tube at the end designated *a* (Fig. 5, *B*). The Y-tube was then placed in position in the dark. Over one arm was laid a red glass, over the other arm an orange glass, and then the screen was drawn from the window to allow the light rays to strike the tube in the direction shown in Fig. *B*. Tests were made about five minutes apart. After each, the return of the lobsters to the (*a*) end of the tube was induced merely by reversing the tube so that the end (*a*) was

toward the window; the position of the red and orange glass was also reversed. The distribution at the end of each test was as follows:

TEST.	RED ARM.	STEM.	ORANGE ARM.
1.....	o	o	10
2.....	o	1	9
3.....	o	1	9
4.....	o	2	8
Totals.....	o	4	36

Case 2—Next, green and blue glass plates were substituted for the red and orange, the method of the experiment otherwise remaining the same, and the green and the blue glasses were reversed in position at the end of each test. A series of four tests showed the following results: Green arm, 11; stem, 2; blue arm, 27.

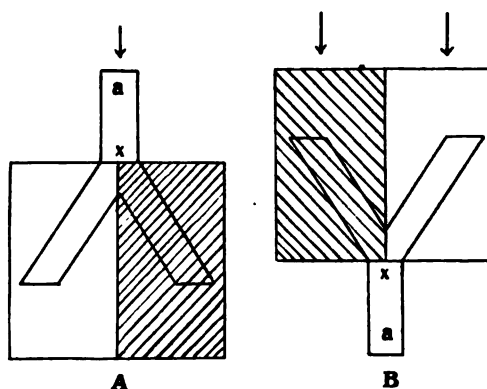


FIG. 5. Showing the Y-tubes as set up for experiment. The arrows indicate the direction of the light rays. The cross-hatched areas represent the glass plates of the darker color laid over the arms of the tubes. The ends designated *a*, represent the starting point for the negatively reacting (A), or the positively reacting (B), larvæ.

Case 3—One more test of the reaction of this group of positive larvæ was made at this time, which was far more delicate than either of the preceding, for the difference in the intensity of the glass plates used was less. In making a selection of glass slides two were chosen which had been purchased for "red glass." On close inspection, however, and by test with sensitized paper, it was observed that one slide was somewhat lighter in color tone than

the other. These glasses were used in the next experiment. The darker of them may be designated as red, the lighter as ruby. The results of four tests were as follows: Ruby arm, 21; stem, 10; red arm, 9. In the last experiment, with this group of larvæ, it was found that a great intensity of light, striking the red slides, was required to bring about reaction; and that, even then, several larvæ would remain in the region designated \times (Fig. 5, *B*), near the junction of light and dark. These experiments were repeated with both black and white backgrounds for the arms of the Y-tube. The results agreed with great uniformity, differing only in the length of time required for the reaction. From these last experiments we may conclude that the first-stage lobsters, at the age of five hours or less, are extremely sensitive to slight differences in the intensity of light, more so in fact than older lobsters of the first and later stages; for it was seldom with these older lobsters that the delicate reaction to the ruby and the red glasses observed in Experiment 15, Case 3, could be induced.

Experiment 16. Twenty first-stage larvæ, slightly over two days old (for which to light of nearly all intensities reactions on the first and second day had been positive), were put in the glass jar, and this in turn was placed in the dark box. They were submitted to light from a small window one inch wide and two inches high, before which the colored glass plates could be placed so as to illuminate one side of the jar with red, blue, green, or orange rays, as the case might be. The reaction in each of these lights was as follows:

LIGHT.	POSITIVE.	NEGATIVE.
Red.....	20	0
Orange.....	20	0
Green.....	19	1
Blue.....	18	2
White*.....	15	5
Day.....	3	17

* Subdued daylight passing through one or two thicknesses of white paper.

Here it is shown that the negative reaction to lights of great intensity, which was first discovered in larvæ thirty hours old (Experiment 14, Case 1), and which, as we shall see, persists for a variable length of time, has become accentuated and remains for the time permanent. The next series of observations were made upon lobster larvæ on the fourth day after hatching. Many of them

were nearing the moulting-period and preparing to pass into the second stage.

Experiment 17—July 17, 8:30 a.m. About one hundred fourth-day, first-stage lobsters (Group A) were taken from one of the hatching bags and placed in the glass jar in the dark box. The majority reacted positively to daylight through the small window. At 1 o'clock, when examined again, about one-half of them were reacting negatively. The jar was then removed and placed in the light of the west window where the intensity was greater. At once every larva became negative in reaction.

In order to determine whether this mode of reaction was a natural incident in the life of the larvæ of this age, or whether the response had been induced as a result of their having been so long subjected to experimentation, twenty-five first-stage larvæ (Group B) were removed from the same group as that from which the larvæ mentioned above were taken. When these twenty-five were put in a glass jar and placed in the west window beside the group mentioned above, they gave a positive reaction. After five minutes, half were positive and half negative. At 5:30 the sun was low and the light weak, but all the larvæ gave a negative reaction, which persisted, as did the negative response in Group A mentioned above, until far into the twilight.

It may be further noted in this connection, that five of the larvæ which reacted negatively in the afternoon were placed in absolute darkness for four and a half hours. It was believed that the positive reaction might be renewed; but this was not the case when they were again brought into daylight of several intensities.

Experiment 18. Case 1—July 20, 4 p.m. A number of fourth-day, first-stage larvæ were removed from the hatching bag and put in the glass jar. This was placed in the dark box and the larvæ submitted to red light through the three by three inch window. The resulting reaction was positive and remained so even when the intensity was still further diminished by inserting numerous sheets of paper behind the red glass. Finally, a point was reached where the positive orientation was lost and a homogeneous scattering occurred. When the intensity of the light was again increased, the positive orientation returned; but, with a still greater increase in intensity, this response became again less definite, and finally, in the more intense blue and white light, the negative reaction again appeared.

Case 2—In the evening, when other observations were made upon the same group under the influence of the acetylene light, burning dimly, the reaction in the glass jar was positive under all the colored glass plates. When the intensity was increased by substituting a lamp which burned more brightly, the group divided, half going to the positive and half to the negative side. When the intensity was increased still further (reinforced by a brilliant oil burner and reflector) a greater number gave a negative reaction. As it afterward transpired, the larvæ used in these last tests did not moult to the second stage until on or after the fifth day.

Case 3—July 23, 1:20 p.m. Fifty fourth-day, first-stage larvæ were put in the glass jar and placed in the dark box. In the red light the reaction was definitely positive. The reaction under the different intensities obtained by colored glass plates may be tabulated as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	50	0
Orange.....	47	3
Green.....	43	7
Blue.....	36	14
White.....	23	27

Case 4—July 31, 10 a.m. Twenty-eight first-stage and second stage larvæ of the fifth day (all nearly ready to moult to the second stage) were put in the glass jar and placed in the dark box. Under lights of different intensities the results were as follows:

LIGHT.	POSITIVE.	NEGATIVE.
Red.....	28	0
Orange.....	22	6
Green.....	18	10
Blue.....	12	16
White.....	14	14
Daylight.....	0	28

In this particular case it was observed that under the orange light the negative larvæ were of the second stage, while those which retained for the longest time the positive reaction (in the case of the blue and white glasses), were the lobsters which were nearest to the moulting-period. When fresh, clean larvæ, which had moulted into the second stage within a very few hours, were selected and submitted to several different intensities of light, they invariably gave the negative reaction.

Case 5—July 23, 1 p.m. Twenty fifth-day, second-stage larvæ were taken from one of the hatching bags and put in the glass jar. This was placed in the dark box and the larvæ were submitted to illumination from the red light. There was some random swimming, but the general reaction was positive, except in white light, in which three were positive and seventeen negative. Next, the jar was removed from the dark box and placed on the west table in subdued sunlight. Here the reaction was definitely negative. At 4:30 when the jar was returned to the box (at this time in the afternoon the light was much less intense than earlier) a positive reaction was obtained in red, orange and green light.

Conclusions from Experiments 16, 17, 18: From the result of the last three experiments the following tentative conclusions may be drawn. The general negative reaction to light of great intensity, begins on about the third day of the first stage, continues for the most part uninterruptedly until the moulting-period is near; just before the moult the reaction becomes indefinite or, more often, positive; directly after the moult into the second stage (which occurs on the fourth or fifth day of the first-stage-period), the reaction to lights of nearly all intensities again becomes definitely negative.

2. *Second Larval Stage.*

Experiment 19. Case 1—July 19, 8:30 a.m. Observation of a group of sixth-day, recently moulted second-stage larvæ demonstrated that a negative reaction took place when the larvæ were put in the glass jar and placed in the dark box. This was true for daylight coming through the three by three inch window, and in both blue and green light. In the case of orange and yellow light, however, the reaction was similar to that in either yellow or orange, but perhaps less definite. It may be here recorded that a group of first-stage larvæ, about one and a half days old, subjected at the same time to these conditions, gave a positive reaction, not only in orange, but also in blue, and even to white light. These reactions took place on both black and white backgrounds, but they were more definite on white. But when the stimulus of the orange rays was continued for ten minutes or more, in this case also, the negative reaction began to appear again and many larvæ came to the room side of the jar.

Case 2—July 23, 5 p.m. The larvæ used in this case were of the seventh-day group of the second stage, having been taken from the hatching bag at 9 a.m. At 5 p.m. under red, orange, green, blue and white lights, entering through the three by three inch window, all were definitely negative. They had also shown a negative reaction in several intensities of light in the morning. At 7 p.m. further observations were made on the same group of larvæ. The following quotation is from the daily note book.

"July 23, 7 p.m. One of the best demonstrations of the persistency of the negative reaction of these seventh-day larvæ was exhibited this evening. Larvæ taken from the hatching bags at 9 a.m. have reacted negatively at every observation during the day. At 7 p.m. it was observed that this group, which still remained in the glass jar near the west window, continued to present a definite negative reaction. This negative response continued until 7:55 p.m., when the light became too faint to determine either a body or a progressive orientation. Here it is to be observed that the negative reaction on the part of these second-stage larvæ was continued through a long series of gradually diminishing intensities of light. After all signs of body-orientation or progressive orientation had vanished in the case of the group of larvæ mentioned above, the intense light from the acetylene lantern was suddenly thrown open one side of the glass jar. A most definite negative reaction resulted. This response, it will be observed, is different from that recorded in Experiment 14, Case 3, for in the latter case the sudden illumination determined a definite positive reaction."

Experiment 20. Case 1—July 24, 9 a.m. Thirty eight-day, second-stage larvæ were taken from one of the large bags and put in the glass jar in the dark box. The time of moulting into the third stage was near at hand, and many of the individuals were already "fuzzy" and sluggish in their movements. Illumination through the three by three inch window, by the colored lights, gave these reactions:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	30	0
Orange.....	27	3
Green.....	17	13
Blue.....	13	17
Day.....	13	17

Before we state the next case, one consideration must be noted. In the previous pages, use has been made of such terms as "third-day," "seventh-day," and "eighth-day" larvæ, to distinguish the age, and roughly the stage, of certain groups of lobsters. Because of the use of these terms, it must not be supposed that there is always a constant relation between the age and the stage of the larvæ. Among the larvæ of a single group which have been hatched and have developed under similar conditions, a fairly constant relation between the age and stage is invariably maintained. But for different groups of larvæ, this correlation does not necessarily exist, for it is entirely possible, and indeed it very frequently happens, that a group of seventh-day larvæ may be in the third stage, while a lot of eight-day individuals are in the second stage. The differences in rate of development are due to such factors as water density, temperature, food-supply, and conditions of light and darkness, which, as the writer has shown (HADLEY '06b), may act either directly upon the body processes, or indirectly by favoring or preventing the growth of various body parasites such as diatoms, protozoa, and algæ that naturally develop in profusion on the bodies of the young larvæ. This explanation will perhaps make clear why, in the following case, we apparently retrace our steps to consider the case of seventh-day larvæ. In point of fact, these larvæ were, at the time of experimentation, somewhat further developed than were the eighth-day larvæ mentioned in Case 1.

Case 2—July 20, 9 a.m. Twenty seventh-day larvæ (eight second-stage, twelve third-stage) were removed from the hatching bag, put in the glass jar, placed in the dark box and illuminated by the light through the three by one inch window. After a half hour, observation showed that the larvæ were equally divided between the window side and the room side of the jar. After five minutes' exposure to red light, thirteen larvæ were positive and seven were negative. When, however, the amount of light was increased by opening the large three by three inch window, only three larvæ remained positive while seventeen became negative. This proportionate reaction endured for several hours, or until observation ceased.

Case 3—July 20, 8 p.m. Twenty seventh-day, early third-stage larvæ were taken from one of the hatching bags, placed in the glass jar, and illuminated by an acetylene light. A more or

less scattering negative reaction at first resulted. When the amount of light was increased by supplementing the acetylene with a brilliant oil burner the response was more definitely negative.

Case 4—July 21, 9 a.m. Twenty-two eighth-day, early third-stage larvæ were taken from one of the hatching bags and put in the glass jar in the dark box. When subjected to subdued daylight through the three by one inch window, sixteen out of twenty-two gave the negative reaction. In orange light the reaction was seventeen negative, five positive; in red light eighteen negative, four positive. Here attention may be called to the fact that these third-stage larvæ gave a negative reaction to practically the same intensity of light as determined a positive response for larvæ in the late second stage.

Case 5—August 3, 2 p.m. Twenty eighth-day, early third-stage larvæ were taken from the hatching bags and put in the glass jar in the dark box. They were submitted to the colored lights, with results as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	8	12
Orange.....	6	14
Green.....	3	17
Blue.....	2	18
White	6	14
Day.....	0	20

Conclusions from Experiments 19 and 20: The conclusions which we draw from the two foregoing experiments support further those formulated for Experiments 16, 17 and 18, on p. 228. In Experiment 20, Case 1, was observed the definite positive response which was manifested toward the end of the second larval stage when the moulting-period was near. In Case 2, where a group of larvæ which included individuals of both the second and third stages was used, it was observed that the reaction was either positive or negative; and that those larvæ which gave the negative reaction most definitely or gave it first were usually the larvæ of the early third stage. In Cases 4 and 5, in which only third-stage larvæ were employed, it was observed that, in general, the reactions to lights of nearly all intensities were negative. As in the case of the first-stage larvæ, it was found that the reaction of second-stage larvæ, just before the moulting-period, usually changed from negative to positive, and again became negative at the beginning of the third larval state.

3. *Third Larval Stage.*

By the ninth day it is only in exceptional cases that the larvæ have not entered the third stage; and it frequently happens that they are nearly ready to enter the fourth. The swimming of the third-stage larvæ is much like that of the earlier stages except that in the third stage there is greater difficulty in using the swimmerets of the thoracic appendages, especially during the last part of the stage. One reason for this is the fact that, as the larvæ grow older and larger, they more often play the host to multitudes of diatoms, algæ and protozoa which gather in such quantities as seriously to interfere with the processes of swimming and eating. In the preparation for the moult from the third to the fourth stage, moreover, occur the most important changes that the young lobster undergoes in the course of its life. These changes appertain not alone to modifications in the external form of the body and to the form and functions of many of the body appendages, but also to points of internal structure. Among the changes during this period of metamorphosis we may enumerate the following as important in connection with our study of behavior: (1) The loss, in the moult from the third stage, of all functional swimming attachments of the thoracic appendages; (2) the great development of both the first and second pairs of antennæ and of the chelipeds; (3) the accession of functioning swimmerets on the under side of the second to sixth abdominal segments; (4) a great change in the form of the body, and a consequent modification of the manner of swimming.

In view of these important changes, which are taking place in the anatomy of the lobsters as they pass from the third into the fourth stage, it does not appear unjustifiable to believe that these processes have an influence on the behavior of the larvæ even before they emerge in approximately the adult structural type, endowed with a new body form, new functional apparatus and new reactions. We shall now undertake a study of the behavior of the third-stage larvæ as they approach and finally pass this most critical period of their life history.

Experiment 21. Case 1—July 22, 9:30 a.m. Thirty ninth-day, third-stage larvæ were removed from the hatching bag, put in the glass jar and placed in the dark box. Under stimulation by the red rays, although there was no definite positive reaction, most of

the larvæ swam about at random on the window side of the jar. When orange glass was substituted for red, half of them came to the room side of the jar. In the case of green glass, a few more reacted negatively, and when blue glass was substituted for green, all but five larvæ gave a negative response. These five did not manifest a definite positive reaction, but swam at random on the window side of the jar. When the colored glasses were removed and the larvæ were submitted to the influence of diffuse daylight through the small window, all reacted negatively.

Case 2—August 4, 9 a.m. Twenty ninth-day, third-stage larvæ were taken from one of the hatching bags and placed in the dark box. Stimulation by the colored light resulted as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	6	14
Orange.....	3	17
Green.....	2	18
Blue.....	2	18
White.....	0	20
Daylight.....	0	20

Case 3—In the present case it was attempted to learn whether the sign of the photopathic reaction in the larvæ of this stage corresponds to the sign of their phototactic reaction. To this end, ten ninth-day, third-stage larvæ, fresh from the hatching bag, were placed in the glass-bottomed box *B*, which was set over the light-shaft and mounted upon colored glass plates. After each observation either a period of five minutes was allowed for a uniform distribution of the larvæ to take place, or the box itself was reversed, leaving the glass plates in the same order. In other instances the order of the glass plates was changed. During this experiment the water in the box was eighteen to twenty mm. deep. The results are presented below:

RED.	ORANGE.	GREEN.	BLUE.
4	0	1	5
1	0	2	7
RED.	ORANGE.	BLUE.	GREEN.
2	1	3	4
1	1	4	4
RED.	BLUE.	GREEN.	ORANGE.
1	5	3	1
2	2	3	3
BLUE.	RED.	GREEN.	ORANGE.
6	0	3	1
5	1	2	2

The larvæ which were used as stated above, and which presented a positive photopathic reaction in every instance, were next transferred to the glass jar and placed in the dark box. Here, and in tubes, the assumed phototactic reaction was uniformly and definitely negative; and this was true in the case of lights which were both of greater and of lesser intensity than in the tests above mentioned.

Case 4—To confirm the results obtained in Case 3, similar tests were made with another group of ninth-day, third-stage larvæ, fresh from the hatching bag. Notwithstanding the fact that this series of observations was not started until 5 o'clock in the afternoon when the light was fading, the results were similar to those obtained in Case 3. That is to say, the photopathic reaction was definitely positive, but the phototactic reaction, as shown when the larvæ were transferred to the glass jar in the dark box, was as definitely negative.

Experiment 22—The following experiment and observations concern the tenth-day, third-stage larvæ. Most of these lobsters were well along in the third stage, and many were covered with body parasites.

Case 1—July 23, 9 a.m. Thirty tenth-day, third-stage larvæ were transferred from one of the hatching bags to the glass jar and placed in the dark box. After having been submitted for one-half hour to light coming through the red glass (three by one inch window), the reaction was uniformly negative. In the case of orange, yellow, green, blue and white light the results were the same. In all of these reactions, however, one fact was noticeable, the body-orientation of these larvæ was much less definite than in any previous case of the same or earlier stages.

Case 2—July 26, 9 a.m. A mixed lot of thirty third-stage larvæ, most of which were ten days old, although some were older and some younger, were transferred from the hatching bag to the glass jar. When submitted to the colored lights in the dark box, the following results were obtained:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	3	27
Orange.....	13	17
Green.....	8	22
Blue.....	13	17
White.....	0	20

In consideration of the apparent fluctuations in the sign of reaction manifested by the above-mentioned larvæ, it may be noted that these lobsters represented a group in which some were "early," others "advanced," third-stage larvæ. Indeed many were approaching the third moulting-period; the significance of this for the behavior of the larvæ we shall consider in the next few cases.

Case 3—July 27, 2 p.m. Thirty eleventh-day, third-stage larvæ were transferred to the glass jar and placed in the dark box. Under colored lights, although the general reaction was negative, many were positive. Experiments made upon the larvæ in the glass-bottomed box *B* to determine the photopathic reaction at this time, showed that the larvæ gave neither a definitely positive nor a definitely negative reaction. Other tests indicated a definitely positive reaction. When, however, light was admitted to the box through the end window (as well as through the bottom), first from the red end, then from the blue end, of the box, there resulted a definite negative phototactic response. The arrows show the direction in which the light entered the box.

→ RED.	BLUE.	ORANGE.	GREEN.
1	2	1	6
1	1	0	9
0	0	0	10
→ RED.	ORANGE.	GREEN.	BLUE.
0	0	0	10
0	0	1	9
RED.	ORANGE.	GREEN.	BLUE. ←
5	1	2	2
6	0	2	2
9	1	0	0

The foregoing cases demonstrate that these larvæ manifested a definitely negative phototactic reaction under the conditions of illumination described; and that, by those rays which had a directive influence, they could be driven into a region of either greater or lesser light intensity, as represented by the blue and by the red ends of the box, respectively. It might be argued that, so long as the eyes of the larvæ are homolaterally stimulated, variations in intensity can not cause or change the orientation, and that orientation results only from a heterolateral stimulation. But this is by no means true, for it has been noted in the foregoing pages, and it will be further demonstrated, that slight differences in intensity,

when coincident with a homolateral stimulation, may even reverse the index of progressive orientation.

Case 4—July 24, 9 a.m. Thirty-five eleventh-day, third-stage larvæ were transferred from the hatching bag to the glass jar and placed in the dark box. The reactions to the colored lights were as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	15	20
Orange.....	16	19
Green.....	8	27
Blue.....	8	27
White.....	7	28

Next, the jar was placed in full daylight, on the table before the west window. All larvæ came to the room side. In this case there were seven larvæ which became the special object of observation, since they invariably manifested a positive reaction until they encountered daylight. This group was set aside, and before night four of the seven had moulted into the fourth stage; consequently their exceptional behavior was due to the fact that they were in a different physiological condition than the majority of the group used in *Case 4*.

Experiment 23. Case 1—In this experiment is continued the examination of the reactions of other twelfth-day larvæ which were approaching the third moulting-period. Twenty-three larvæ were placed in the glass jar and observed under the influence of the colored lights in the dark box. The results were as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	6	17
Orange.....	15	8
Green.....	6	17
Blue.....	4	19
White.....	3	20

Case 2—At 3:30 p.m. Ten larvæ from the above groups were transferred to the glass-bottomed box *B*, which was set up over the light-shaft upon the colored glass plates. The results were as follows: Blue, 19; green, 3; orange, 4; red, 4. During the course of the day, many of these ten larvæ moulted to the fourth-stage.

Case 3—July 29, 9 a.m. By this date there were very few third-stage larvæ left in any of the groups whose actual age was known. Indeed there are few cases in which the development is so slow that the third-stage larvæ endures to the thirteenth or

fourteenth day. In this particular instance, twenty larvæ were transferred to the glass jar and placed in the dark box. The resulting reactions to the colored lights were as follows:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	16	4
Orange.....	16	4
Green.....		
Blue.....	13	7
White.....	9	11
Day.....	0	20

It may be observed in the account of the last three experiments how the general reaction of the third-stage larvæ has gradually changed from negative to positive; and how it requires an increasingly greater intensity of light to determine a negative response in the larvæ which are approaching the fourth stage. In the next case the culmination of this gradual change is reached, since the third-stage larvæ almost uniformly manifest a positive reaction which is as definite as that of the newly-hatched larvæ.

Case 4—July 30, 2 p.m. Thirty fourteenth-day, third-stage larvæ secured from a group in which nearly all had entered the fourth stage, were transferred from the hatching bag to the glass jar and placed in the dark box under the influence of colored lights:

COLOR.	POSITIVE.	NEGATIVE.
Red.....	30	0
Orange.....	30	0
Green.....	30	0
Blue.....	30	0
White.....	28	2
Day.....	23	7

It is here observed that, when as indicated above, the jar was removed from the dark box and placed on the west table in daylight, only seven larvæ became negative. All the others remained positive, even in this light of great intensity. This case represents the strongest and most definite maintenance of the positive reaction in late third-stage larvæ ever observed by the writer. These larvæ moulted into the fourth stage very soon after the above observations were made.

Case 5—In the following test other members of the group of larvæ used in the previous case were employed. The aim was to learn whether or not the photopathic reaction in these larvæ was in agreement with the phototactic reaction described in Case

6. The larvæ were placed in the glass-bottomed box over the light-shaft; fifteen minutes was allowed for the first orientation, and five minutes was given for each of the others:

AFTER	BLUE.	GREEN.	ORANGE.	RED.
15 minutes.....	6	2	2	0
20 minutes.....	6	1	1	2
25 minutes.....	4	1	5	0
30 minutes.....	4	5	0	1
35 minutes.....	3	7	0	0
40 minutes.....	2	7	0	1
Totals.....	25	23	8	4

It thus appears that the photopathic reaction of the larvæ was definitely positive. After this series of observations the larvæ were returned to the glass jar and placed on the west table. In the faint daylight which remained, the positive reaction was manifested and continued as long as the light lasted.

Conclusions from Experiments 20, 21, 22 and 23: As has been noted, these experiments deal with the reaction of larvæ as they pass through the third and enter the fourth stage. In Experiment 20 (Cases 2, 3, 4 and 5) it was shown that, in general, the majority of early third-stage larvæ reacted negatively, frequently to light of weak intensity, and invariably to light of greater intensity. In Experiment 21 it appears (1) that this negative response was fairly characteristic of the early third-stage larvæ; (2) that, notwithstanding this negative phototactic reaction, the photopathic response might be definitely positive (Experiment 21, Case 3) thus appearing to indicate that, at least at a certain period in the life of the third-stage larvæ, a positive photopathic reaction and a negative phototactic response may be given by the same individual. Experiment 22 demonstrates (1) that, as the third-stage advanced, the positive reaction, was more frequently and more easily determined by light of all intensities (Case 2), and that an increasingly strong illumination was required to bring about a negative reaction (Case 4); (2) that the photopathic response, if anything, remains throughout the stage, positive (Case 3), while the sign of the phototactic response may change with the intensity of the light (Cases 2 and 4).

In Experiment 23 it is observed that the negative reaction to strong light was still prominent in the behavior of the twelfth-day

larvæ (Case 1), while on the thirteenth and fourteenth days, as the moulting-period to the fourth stage approached, the negative reaction was less easily determined (Cases 3 and 4). It was observed furthermore, that these larvæ continued to manifest a very definite positive photopathic response (Case 5), and that this was maintained until the end of the stage-period.

General conclusions on the behavior of larvæ of the first three stages—As the larvæ, after the very definite positive photopathic and phototactic reactions characteristic of the first part of the first larval stage, pass on through the first stage-period, lights of low intensity (red, orange, twilight, etc.), gradually lose their efficiency in bringing about a positive phototactic reaction, while, on the other hand, lights of a greater intensity (green, blue, daylight, etc.) determine, more and more easily, a negative response. This negative phototactic response, which may enter on the third day of the first stage-period, changes again to positive as the first-stage larvæ draw near the first moulting-period. At this time, the lights of low intensity are again effective in bringing about a positive reaction, which is maintained until the larvæ have moulted into the second stage.

While the photopathic reaction of newly moulted second-stage larvæ remains positive, the phototactic response is more often negative, and this negative response is commonly maintained until toward the end of the second stage-period. At this time, as was observed in the first stage-period, a positive reaction again becomes manifest as the larvæ approach the period of moulting into the third stage.

While the positive photopathic reaction still obtains, the newly moulted third-stage larvæ commonly manifest a negative phototactic reaction, and this, as was the case with the second-stage larvæ, is retained until the moulting-period into the fourth stage approaches. At this time the reaction again becomes positive, and continues so until the larvæ have entered the fourth stage. These general points in the behavior may be illustrated by the following diagram (Fig. 6).

The foregoing facts serve to emphasize further the statement made on an earlier page, that we can not justly say that the larvæ of *Homarus* are positive to light or negative to light, or that they react in this way to intensity, and in that way to the directive influence of the light rays. But these observations do show that

the larval lobsters manifest a type of behavior which includes widely varying kinds of reaction, even to the same stimulus. The point has been, not to learn what reaction the lobster larvæ give to light, but to ascertain the conditions which so play upon the mechanism of these organisms as to produce the wide range of responses observed. The causes of the daily and the hourly variations in the kinds of reactions manifested by organisms is a field which is, even at the present day, largely given up to speculation, and all sorts of explanations have been brought forward from the view of the rhythmical succession of certain movements resulting from purely internal stimuli, to the view of cycles of change in certain metabolic products under the influence of external stimulation, and their consequent reaction upon the nervous processes of the organism. The fact of variations in the reactions of larvæ of the European lobster (*Homarus vulgaris*) has been noted by

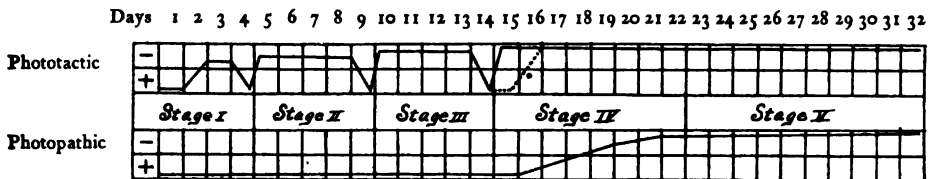


FIG. 6. Diagram recapitulating the nature of the phototactic and photopathic reactions of lobsters in the first five stages. The dotted line in the upper series indicates that the early fourth-stage lobster may give a positive phototactic reaction to light of very great intensity. For further explanation, see General Conclusions on p. 239.

BOHN (1905, p. 10). After having made several observations upon recently hatched larvæ, he comes to the following conclusion. "De ces diverses observations, il semble résulter que le sens de déplacement des larves de homard subit des variations occellantes de signe, qui, bien que influencées par l'éclairement actuel sont en relation avec les heures de la journée."

Although certain phases of behavior in some marine animals may be explainable on the ground of rhythmically recurring reactions which bear a certain relation to the hours of the day, the present writer's experience with larvæ of all ages and stages of the American lobster makes it quite impossible to attribute the variations in the reaction of lobster larvæ to such causes. The hours of the day, except as they are accompanied by corresponding differences in the intensity of light, have nothing to do with

the form of reaction displayed by the lobster larvæ. This is readily shown, first, by the fact that, at any corresponding time on two successive days (and especially when a moult has intervened), the reactions of the same larvæ may be quite dissimilar. Here the reactions are explainable on the grounds of (1) the stage of the larvæ and their age in the stage-period; and (2) the intensity of the light and of other stimuli which are brought to bear. This conclusion is shown furthermore by the fact that larvæ at corresponding times in the different stage-periods usually manifest similar types of reaction. Thus does it appear that, although the diverse forms of reaction are partly due to the differences of intensity in actual illumination, the underlying cause is some physiological change which the larvæ undergo as they gradually approach and pass the crises of their moulting-periods.

4. *Fourth Stage.*

We come now to a consideration of the reactions to light of the fourth-stage lobsters. It has been observed in previous pages that the most striking change, not only in body-form but also in life-habits, which takes place in the life of the lobster, occurs during the transition from the third to the fourth stage. It is the aim of the present section to analyze the reactions of the fourth-stage larvæ and to exhibit the conditions which determine or modify these reactions.

In the previous pages the lobsters under consideration have been referred to as the "second-day" or the "fifth-day" larvæ, etc., as the case might be, and this terminology was of advantage, because the first three stage-periods are so brief that changes may occur even in two consecutive days. The fourth stage-period, however, is much longer (usually eight to twelve days) and the differences in reaction on two consecutive days may be slight or inappreciable. For this reason, then, in the following consideration we shall divide the fourth stage-period into three parts, viz: the early, the mid, and the late fourth stage-period.

Experiment 24. Reactions of early fourth-stage lobsters. Case 1. Photopathic reactions—July 28, 10 a.m. Ten early fourth-stage larvæ were put in the glass-bottomed box *B* and this was placed over the light-shaft. The arrangement of the colored plates and the resulting orientations were as follows. The results

indicate that the early fourth-stage lobsters show a slight tendency to remain in the more brightly illuminated areas.

RED.	ORANGE.	GREEN.	BLUE.
1	1	2	6
2	2	1	5
2	3	2	3
—	—	—	—
5	6	5	14
RED.	ORANGE.	BLUE.	GREEN.
4	1	2	3
2	2	2	4
0	2	5	3
0	1	4	5
—	—	—	—
6	6	13	15
GREEN.	BLUE.	ORANGE.	RED.
2	4	1	3
1	4	2	3
3	3	2	2
—	—	—	—
6	11	5	8
<i>Totals.</i>			
BLUE.	GREEN.	ORANGE.	RED.
38	26	17	19

Case 2. Phototactic reaction—August 7, 5:30 p.m. Ten early fourth-stage larvæ were placed in box *B* and the end window of the box was opened to the diffuse light of the west window. As has been explained, this box was so constructed that in a moment glass plates could be slid through the cover, and into such position that they would divide the floor area of the box between the ends into four equal parts. Beginning with the end toward the light these may be numbered 1, 2, 3, 4, respectively, and the results showing the imprisonment of the larvæ in two instances, may be recorded as follows:

1.	2.	3.	4.	1.	2.	3.	4.
2	2	0	6	2	1	2	5
7	0	0	3	0	1	2	7
2	0	2	6	0	0	1	9
0	0	2	8	0	0	3	7
—	—	—	—	—	—	—	—
11	2	4	23	2	2	8	28

In the second of these instances an acetylene light was used, the intensity being diminished by inserting a red glass between the burner and the window in the end of the box toward the light.

Case 3. Phototactic reaction—August 9, 3:40 p.m. Ten early fourth-stage lobsters were transferred from the confining bag to box *B*, and this was placed with the end toward the west light. In this case, colored glass plates were placed at intervals in front of the end window to modify the intensity of the light entering the box. A five-minute intermission was allowed between observations. The results, which clearly establish a negative phototactic reaction, are presented in the following table:

COLOR.	1.	2.	3.	4.
	2	1	2	5
	1	1	2	6
	2	1	3	4
	0	0	2	8
Orange	5	3	9	23
	0	1	2	7
	0	1	4	5
	1	3	2	4
	0	1	1	8
Red.....	1	6	9	34
	1	0	1	8
	0	0	0	10
	1	1	0	8
	1	2	2	5
Green.....	3	3	3	31
Totals.....	9	12	21	78

Case 4. Phototactic reaction—In the following case, in which the same lobsters were used the source of illumination was the acetylene light and the intensity of the light which entered the end window of box *B* was modified in two ways: (1) by the colored glass plates placed between the light and the window in the end of the box; (2) by the distance of the light from the box. The results, which demonstrate a definite negative phototaxis, were as follows (in all cases the figure 1 indicates the division of the box nearest the light; 4 the division farthest from the light):

COLOR.	DISTANCE.	1.	2.	3.	4.
Red.....	2 inches.....	3	1	2	4
		1	0	1	8
		1	2	3	4
		1	1	1	5
	Totals.....	6	4	9	21
Red.....	6 inches.....	2	1	1	6
		1	3	2	4
		3	0	1	6
		1	2	2	5
	Totals.....	7	6	6	21
Red.....	12 inches.....	3	1	2	3
		4	2	1	3
		1	3	2	4
		2	4	4	2
	Totals.....	10	8	9	12
Blue	12 inches.....	0	1	4	5
		1	1	3	5
		3	2	0	5
		2	2	0	6
	Totals.....	6	6	7	21
Blue.....	2 inches.....	2	0	1	7
		1	1	2	6
		2	1	2	5
		2	1	3	4
	Totals.....	7	3	8	22
Totals.....		36	27	39	97

Case 5—One observation on the behavior of the early fourth-stage lobsters is difficult to harmonize with the reactions mentioned in the previous cases. When at night the rays from an acetylene light were brought to bear upon very early fourth-stage lobsters, swimming in the confinement bags, they would sometimes swim directly toward the light. This reaction was often so strongly manifested that the natural rheotactic response to the influence of the water current circulating in the bags was quite obscured in the areas of greatest illumination, because the young lobsters followed—so to speak—the course of the rays from the acetylene lantern. If this reaction represents a true phototactic response, then it must be said that very early fourth-stage lobsters may, under appropriate conditions of stimulation, respond positively to the directive influence of light, not, as do the earlier stages or the late fourth-stage by turning from the light, but by “heading”

into it. In an earlier paper (HADLEY 1906b), the writer has assumed this to be a true phototactic response. One other instance which appears to support this view may be recorded as follows.

Case 6—Ten sixteenth-day, fourth-stage lobsters were placed in a large slender dish, which was set in the dark box. The larvæ manifested no tendency to undergo either body-orientation or progressive orientation. Next, the same lobsters were placed in the glass-bottomed box, now lined with white paper, which greatly intensified the light within. This box was put with the end window toward the bright sunlight, and the records of five trials (ten larvæ in each) indicated that, when the light was sufficiently intense, the early fourth-stage lobsters might give a positive phototactic reaction. In this instance twenty-six larvæ were positive, twelve negative, and twelve neutral.

When the white paper was removed, and four more tests were made, the results showed that twenty-five larvæ were negative, six positive, and nine neutral.

Experiment 25. Reaction of mid-fourth-stage lobsters. Case 1. Phototactic reaction—August 10, 3:30 p.m. Ten mid-fourth-stage lobsters were transferred from the hatching bags to box *B*, and the experiment was continued in daylight as in Experiment 24, Case 2. The results show a definite negative phototactic reaction, and may be tabulated as follows (similar results were obtained when a white lining in the box was used, though in this case, they showed a less definitely negative reaction):

COLOR.	1.	2.	3.	4.
Orange.....	1 0 0 1	1 1 0 1	1 2 1 2	7 7 9 6
Totals.....	2	3	6	29
Blue.....	0 1 1 1	1 0 1 1	2 1 2 1	7 8 6 7
Totals.....	3	3	6	28
Ruby.....	0 0 1 1	0 2 1 0	1 1 4 3	9 7 4 5
Totals.....	2	3	9	25
Grand Totals.....	7	9	21	82

Case 2. Photopathic reaction—August 9, 3:30 p.m. Ten fourth-stage lobsters were removed from one of the confinement bags and placed in 16 mm. of water in the glass-bottomed box. The glass plates were arranged in the order given below, and tests were made at five-minute intervals. The results, which showed a diminished tendency to remain in the areas of greatest illumination, are represented in the following table:

RED.	ORANGE.	GREEN.	BLUE.
3	2	1	4
4	0	3	3
1	2	1	6
2	2	4	2
2	4	2	2
—	—	—	—
12	10	11	17

When, some hours later, the same lobsters were tested again the results of five trials were as follows: Blue, 13; green, 9; orange, 7; red, 21; apparently in this instance it can not be said that the mid-fourth-stage lobsters were either positively or negatively photopathic. Yet the last instance shows a tendency toward a negative reaction.

Experiment 26. Reaction of late fourth-stage lobsters. Case 1. Photopathic reaction—August 12, 2 p.m. Ten late fourth-stage lobsters were transferred from one of the confinement bags (where the majority had already entered the fifth stage) to the glass-bottomed box which was placed over the light-shaft in order to test the photopathic reaction. In this case nine consecutive tests were made, three minutes being allowed for each orientation. The results, which are characteristic of all other tests, and which show a tendency on the part of the lobsters to avoid the light, may be recorded as follows:

No.	BLUE.	GREEN.	ORANGE.	RED.
1.....	1	2	1	6
2.....	1	0	3	6
3.....	3	0	2	5
4.....	3	4	1	2
5.....	1	2	1	6
6.....	3	1	0	6
7.....	5	3	0	2
8.....	1	1	1	7
9.....	4	2	2	2
Totals.....	22	15	11	42

Case 2. Phototactic reaction—August 10, 3:30 p.m. Ten late fourth-stage lobsters were taken from one of the hatching bags and put in box *B*, which was placed in the dark box so that the end window faced the light, the intensity of light being modified in each case by interposing colored glass plates between the end window and the light. The tests, which were made at three-minute intervals, and which showed a very definite negative reaction, were as follows (in the fourth tests of the first and last sets respectively, one lobster was accidentally killed, thus making the totals incomplete):

COLOR.	1.	2.	3.	4.
	1	1	1	7
	0	1	2	7
	0	0	1	9
	1	0	2	6
Orange.....	2	2	6	29
	0	1	2	7
	1	0	1	8
	1	1	2	6
	1	1	1	7
Blue.....	3	3	6	28
	0	0	1	9
	0	2	1	7
	1	1	4	4
	1	0	3	5
Red.....	2	3	9	25
Totals.....	2	8	21	82

Conclusions on the reaction of fourth-stage lobsters—The observations thus far made upon the behavior of fourth-stage lobsters appear to demonstrate the following points: (1) Throughout the entire fourth stage-period (with the exceptions noted under Experiment 24, Cases 5 and 6), the lobsters manifest a negative phototactic reaction, which is accentuated in the latter part of this stage. This behavior is quite different from the positive reaction which supersedes the negative in the case of second and third-stage larvæ just previous to their moult into the third and fourth stages respectively; (2) This type of reaction after the first part of the fourth stage-period, cannot be reversed or modified, as was

the case in earlier stages, by using different intensities of light (3) The photopathic reaction, which in the early fourth-stage lobsters is definitely positive, changes by the latter part of the stage to negative in the majority of individuals. Thus it can be observed that, just as the third-stage larvæ might at the same time (or successively) manifest both a negative phototactic and a positive photopathic reaction, so may the lobsters of the fourth stage. Other points regarding the behavior of fourth-stage lobsters will receive consideration in connection with the subject of contact-irritability.

5. *Fifth Stage.*

The body-form of the fifth-stage lobster is similar to that in the fourth-stage, and we might therefore expect to find similar types of reaction. It will be seen, however, that there are many points of difference in behavior which are of such a nature that they can not be attributed, either wholly or in part, to changes in body-form or in the swimming appendages. The changes are doubtless the consequence of modifications which have taken place in the body-processes or in the physiological states of the lobsters themselves, and which have resulted from the cumulative stimulation during the earlier life of the lobsters. Generally speaking, it may be said that the reactions of the fifth-stage lobsters are fairly typical for the adult form, and are especially characterized by the light-shunning tendency. This form of behavior could be observed readily by watching the lobsters in their confinement cars; but, for the sake of certainty, the same experiments, to which the larvæ of earlier stages had been subjected, were repeated with the fifth-stage lobsters. Since the reactions did not appear to undergo any noticeable modification as the lobsters passed through the fifth stage, there is no need for considering the early, mid and late fifth stage-periods separately, as was done for fourth-stage lobsters. The type of reaction presented in the early fifth stage-period differs in no way from the behavior of lobsters in the late fifth stage-period; and both are characteristic of the behavior in all later stages.

Experiment 27. Case I. Photopathic reaction—In the first instance, ten fifth-stage lobsters were transferred from one of the confinement bags to the glass-bottomed box and this was placed over the light-shaft. The method used was the same as in pre-

vious experiments. In the second instance the blue glass was removed, and the space where it had lain was left clear, thus permitting the reflected daylight to enter this area of the bottom of the box. The results of both tests show a negative reaction which was more definite in the second instance.

BLU.	GREEN.	ORANGE.	RED.
2	1	2	6
2	1	2	5
3	1	1	5
2	3	2	3
—	—	—	—
8	6	7	19
DAYLIGHT.	GREEN.	ORANGE.	RED.
0	2	2	6
0	3	2	5
1	2	2	5
0	2	2	6
1	1	3	5
0	2	4	4
—	—	—	—
2	12	15	30

Case 2. Phototactic reaction—Further demonstration of the definitely negative phototactic response of fifth-stage lobsters was given by the experiments on contact-irritability (Exp. 29, p. 256). Here is clearly shown the extreme manifestation of this negative phototactic response, which frequently would have culminated in fatal results by driving the lobsters from deep to shallow water and leaving them stranded where they would certainly have died had they not been returned to the water at the end of the experiments. Here, as has been found in the case of many animals, the total behavior is completely dominated by the light influence. It may be said further that in the case of the fifth-stage lobsters light of different intensities does not cause a change of reaction from positive to negative, or from negative to positive, as was the case in the earlier stages; nor do we ever find the individuals "heading" into the light, as may be the case in the fourth-stage larvæ. For the fifth-stage lobsters any intensity of light which influences their behavior in any degree, determines, under experimental conditions, both a negative body-orientation and a negative progressive orientation.

In the foregoing pages it has been shown that larvæ which were positively photopathic could be made to pass from regions of greater to regions of lesser light intensity by submitting them to

the directive influence of light of sufficient strength. In these cases, it was observed that the photopathic reaction was invariably subservient to the phototactic, although the latter was also very dependent upon a certain optimal intensity for bringing about a positive or negative response. In the following instance we shall observe that, although the directive influence of the light rays is capable of modifying the orientations which relative intensities of light have determined, still the directive influence can not quite obliterate the evidence of a photopathic reaction, as was possible in the younger larvæ. In other words *the tendency of the fifth-stage lobster to "select" the darker regions has become almost as firmly fixed as has the tendency to react negatively to the directive influence of the light rays.* In the first larval stages the photopathic response invariably gives way to the phototactic. In the fifth the two tendencies clash; and the resulting orientation of the lobster is determined, not by one, but by both of these factors.

(A.) *Case 3. Photopathy versus phototaxis*—Ten fifth-stage lobsters were put in box *B*. This was mounted upon the colored glass plates over the light-shaft as in previous experiments. The preliminary observation showed that there was a definite tendency for the lobsters to congregate at the red end of the series of glass plates, thus demonstrating a negative photopathic reaction. Now the window at the red end was opened to diffuse light. After a period of ten minutes, observations of the position of the lobsters were begun, and continued at five-minute intervals. The following results show that, although the negative phototactic response is still manifested, it has been greatly modified by the tendency on the part of the lobsters to avoid the brightly illumined area at the end of the box:

DAYLIGHT.	GREEN.	ORANGE.	RED.
1	4	2	3
1	3	3	3
2	3	3	2
1	3	4	2
1	2	4	3
2	3	3	2
<hr/>	<hr/>	<hr/>	<hr/>
8	18	19	15

In the next case, the end of the glass plate series, which in the previous instance admitted reflected daylight, was covered with a blue glass and the illumination of this area thus rendered less

intense, while the end window of the box (at the red end) remained open, as in the last experiment. The results, which demonstrate that the phototactic reaction had still further overcome the photopathic, were as follows:

BLUE.	GREEN.	ORANGE.	RED.
2	2	4	2
1	3	2	4
3	2	3	2
3	2	2	3
4	3	2	1
2	3	2	3
<hr/>	<hr/>	<hr/>	<hr/>
15	15	15	15

In the last two instances it becomes apparent that the fifth-stage lobsters, unlike the early-stage larvæ, could not be forced, by the directive influence of the light rays, into an area of greater light-intensity. In other words, the tendency to manifest a negative phototactic reaction was not sufficiently strong to overcome the tendency to give a negative photopathic response.

(B.) *Experiment 28. Phototaxis leading to fatal results*—Before bringing to a close this consideration of the reactions to light in lobsters of the fourth and fifth stages, it may be appropriate to introduce the results of some experiments whose aim was to show the extreme nature of some phototactic reactions. In other words, attempt was made to determine whether or not the strong directive influence of the light rays could compel the larvæ so to act that they would do injury to themselves as in the familiar case of the moth that flies into the flame, or of *Ranatra*, mentioned by HOLMES (1906). The reactions of the fourth-stage and fifth-stage lobsters will be considered together.

Case 1. Fourth-stage lobsters—For this series of experiments box *B* was set up as represented in Fig. 7, being supported at one end so that the bottom of the box made an angle of about fifteen degrees with the table. The box was filled with water so that when it was slanted, the water-line did not quite reach the angle made by the bottom and upper end, *B*. In this way there was created an inclined plane, slanting from the window end, *A*, of the box to the higher end, *B*. The water consequently diminished in depth as the end, *B*, was approached. At this end there was an inch or more of the bottom of the box not covered by water. The light from the window, *L*, was reflected into the box by the mirror,

M, for the purpose of discovering whether the larvæ in presenting their negative phototactic reaction, would allow themselves to be driven into the shallow water. By means of a hole in the bottom of the box, the water could be withdrawn very gradually (a few drops a minute), so that if the larvæ persisted in remaining in the

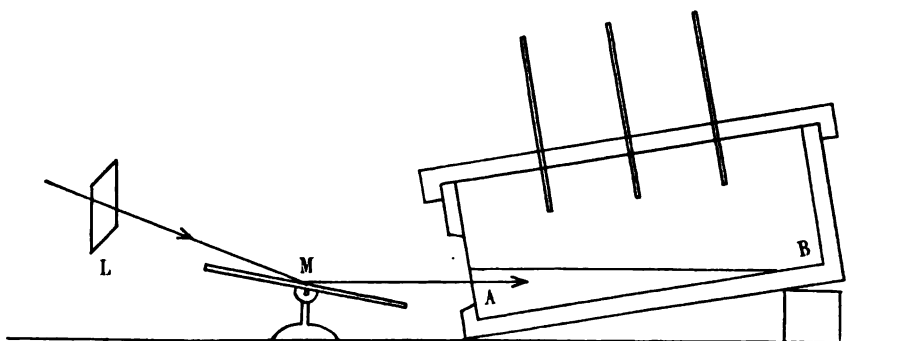


FIG. 7. Diagram of apparatus as set up to test the extreme phototactic reactions, leading, in the case of fourth and fifth-stage lobsters, to fatal results. *L*, source of light; *M*, reflecting mirror; *A*, end of box adjacent to "window;" *B*, end of box not covered with water, where the lobsters were stranded. In the cover of the box are shown the sliding partitions.

shallow area, they would, in the course of a few minutes, be stranded on the dry bottom. Ten fourth-stage lobsters were first used for experiment and the results, ascertained by counts made as in all other cases, were as follows: (The arrow shows the direction of the light coming through the end window of the box, while the numbers at the top of the columns represent the division areas of the box):

TEST.	→ 1.	2.	3.	4.	NUMBER STRANDED.	TIME (after).
1	1	1	3	5	4	5 minutes
2	1	2	1	6	3	10 minutes
3	0	1	1	8	6	20 minutes
4	1	1	3	5	5	50 minutes
Totals.....	3	5	8	24	18	

The results of this experiment and of several others similar to it, show, that out of a total of twenty-four larvæ which gathered

in the area farthest from the light, eighteen allowed themselves to be stranded rather than to retrace their course into deeper water, and in so doing to approach the light.⁴

Case 2. Fifth-stage lobsters—When the same experiment involved the fifth-stage lobsters, the results were similar. The only difference that could be observed was that the intensity of the reaction was greater for the fifth-stage than for the fourth. The result of twelve tests, each with ten lobsters showed the distribution to be as follows: Area 1, nine; area 2, ten; area 3, twenty-one; area 4, eighty, of which seventy were "stranded." These last would have perished, had they not been returned to the water at the end of each successive test.

(C.) *Conclusions concerning the reactions to light of fifth-stage lobsters*—The results of the foregoing experiments on the reactions of fifth-stage lobsters, demonstrate the following points: (1) Like the fourth-stage lobsters, the fifth-stage lobsters are negatively phototactic from the beginning of the stage to the end of it, and this holds good for all intensities of light which cause any reaction whatever. (2) Unlike the early fourth-stage but much like the late fourth-stage lobsters, the fifth-stage lobsters are negatively photopathic from the beginning of the stage to the end. (3) This negative photopathic reaction, unlike the photopathic reactions of the earlier stages (in which case the photopathic reaction was entirely subservient to the phototactic), has itself become a well grounded tendency, and, although it can be modified, it can not be entirely obliterated (so far as its value in causing a certain orientation is concerned) by the tendency to react to the directive influence of the light rays. (4) The intensity and energy with which the late fourth-stage, but especially the fifth-stage, lobsters manifest a negative phototactic reaction may lead to results fatal to the lobsters themselves.

(D.) *Contact-irritability versus reaction to light*—In the preceding section the phototactic and the photopathic reactions, together with some points of their inter-relation, have been considered. We shall now examine that response of lobsters to solid portions of their immediate physical environment which may be ascribed to contact-irritability or thigmotaxis.

It frequently happens that single types of reaction (phototaxis, chemotaxis, geotaxis, and the like) may be studied to best advan-

⁴ It should be noted, however, that the water in no case receded more than 5 to 10 mm. as measured horizontally on the bottom of the box.

tage only when another stimulus of known effect is present and operative. For instance, if the two conditions of stimulation which respectively bring about a photopathic and a phototactic reaction are so arranged as to oppose one another (i. e., by determining opposite reactions in the larvæ), and if the constant effect of one set of conditions is known, then it is possible to form an estimate of the persistency of the reaction determined by the opposed set of conditions. For example, if light rays of low intensity coming through the end of box *B*, resulted in driving the enclosed larvæ, which had just previously given a negative photopathic reaction, to the opposite end of the box, and at the same time forced them from a region of low into a region of high intensity, we should say that the negative photopathic reaction of these larvæ was of slight importance as compared with the phototactic. If, on the other hand, it was learned by experiment that the rays entering the end window of box *B* would not force the negatively photopathic larvæ from the dark into the brightly illuminated end of the box, but resulted in their gathering in the middle of the box (for instance, in the green or orange area) then it might be inferred that the negative photopathic reaction had a greater influence in determining the final reaction of the larvæ, although it was in this case directly and strongly opposed by the tendency to manifest a phototactic reaction. In the following experiments, made to discover the value of contact-irritability in determining the reaction of the larvæ, the principle mentioned above was made use of, and in this instance a combination was made between experimental conditions which would allow the demonstration of contact-irritability, and those which would insure the manifestation of negative phototaxis if no other modifying conditions (such as contact-irritability) were present. But before going farther with the description of the technique of the experiments, a few observations on the behavior of the lobster larvæ under natural circumstances may be considered. This may form a better basis for the consideration of experiments dealing with contact-irritability versus reaction to light under the especially devised conditions to be described.

It might reasonably be imagined that the loss of the swimming branches (exopodites) of the thoracic appendages, which takes place with the entrance to the fourth stage, would at once determine a very radical change in the habits of lobster larvæ. We should surmise that the larvæ would immediately abandon their

pelagic manner of existence and enter upon a more sedentary life among the rocks and weeds of the sea bottom. But this is by no means the case, for never in the life history of the lobster do we find surface swimming more strongly manifested than in the fourth stage, and just after the loss of those accessories without which swimming would have been impossible in any of the earlier stages. The energetic surface-swimming of the fourth-stage lobsters was evident from many observations, made under both natural and experimental conditions. It was observable not only in the large hatching bags but also in the quiet water surrounding the bags and hatching apparatus. One case is especially noteworthy. In July a steam launch, of which the captain lost control, rammed one of the floats which suspended six large hatching bags containing lobsters in various stages. As a result many fourth-stage lobsters were suddenly liberated in the water about the hatchery. When order had been restored, an attempt was made to recover the lost lobsters, and over five hundred of the fourth-stage which were swimming actively at the surface of the water were picked up with scrim nets. A far different phenomenon obtains in the behavior of fifth-stage lobsters under natural conditions. This is illustrated by an interesting sequence of changes in the swimming habits. When the majority of the lobsters in the bags were in the fourth-stage, they usually swam near the surface. As the larvæ moulted into the fifth stage, fewer lobsters were to be seen. The reason for this was ascertainable if one poked with a stick about the mass of weeds and algæ adhering to the sides and bottom of the bag. Here could be found, carefully hidden, a large number of fifth-stage lobsters. By the time all the individuals in the bag had passed to the fifth-stage, scarcely one could be discovered swimming freely. Whenever a number of fifth-stage larvæ were liberated in the open water, it was an interesting sight to observe them swim for a moment, then turning head down, disappear for good in the deeper water—a great contrast to the behavior of the fourth-stage lobsters under similar conditions.

Another set of observations refers to the burrowing instinct of the young animals. When early fourth-stage lobsters were transferred to glass dishes, on the bottom of which was a layer of sand, gravel and a few broken shells, they at first paid no heed to these conditions, but for several days continued to swim as persistently as ever. Finally, however (usually within two or three days after

having been placed in the dish), the lobsters began to plough through the sand of the bottom, especially near the rim of the container, and to construct burrows beneath shells, stones or other objects in the sand. Yet, even after these burrows were completed, the fourth-stage lobsters seldom remained in them, but came out and crawled rapidly over the bottom or swam more or less actively near the surface of the water. When, on the other hand, fifth-stage lobsters were introduced into the dishes containing sand, gravel, and shells they commenced burrowing at once and when the burrows were completed they showed a much greater tendency to remain therein than did the late fourth-stage larvæ. Although the fifth-stage lobsters came out for food, free swimming was seldom indulged in during such sorties. The question now arises as to what conditions or factors cause the energetic surface-swimming of the early fourth-stage lobsters and the bottom-seeking and burrowing habit of the late fourth and the fifth stage. Are these reactions to be explained as phototropic, geotropic, or thigmotropic reactions? Or do all three of these, and perhaps still other factors, unite in determining the final result? While we are not yet prepared to venture an answer to these queries, the records of a few simple experiments which were undertaken to ascertain the value of the part played by contact-irritability in determining the orientation of the fourth and fifth stage lobsters, under certain known conditions, will be presented.

Experiment 29. Fourth-stage lobsters—The technique employed in the present experiment was as follows: One-half of the bottom of box *B*, was sprinkled with sand to the depth of five mm., the box was filled with salt water to a depth of 3 cm., ten early fourth-stage lobsters were introduced, and the box covered. The aim was to learn whether, in the total absence of light, the larvæ would "choose" either the sanded or the clear area. The result of a typical test is presented below. The readings were taken every five minutes, and after each reading the lobsters were caused to distribute themselves about the box:

SANDED AREA.		CLEAR AREA.	
1.	2.	3.	4.
4	3	2	1
2	2	3	3
3	2	2	3
1	1	4	4
—	—	—	—
10	8	11	11
18		22	

These and other tests were made, but in no case was it apparent that the early fourth-stage lobsters showed any preference for the sanded area. When, in another series of four trials involving ten lobsters each, the window at the sanded end of the box, was opened so as to allow the rays to stream through, every lobster but one was driven to the compartment farthest from the light. When this experiment was tried with late fourth-stage lobsters, it appeared that a greater number remained on the sanded area, even in the presence of the light conditions mentioned above. The results of a typical experiment of this sort involving five trials of ten lobsters showed that, while thirty were driven to the clear space, ten remained on the sanded area.

Experiment 30. Case 1. Fifth-stage lobsters—In this instance ten fifth-stage lobsters were placed in box *B* as arranged for the previous experiment, no light being admitted at the end of the box. The record of seven trials separated by a period of from five to ten minutes, showed a decided preference for the sanded areas; while forty remained on the sanded region, only twenty gathered on the clear area.

Case 2—In the next instance the end window at the sanded end of the box was opened to the light, but with a red glass so interposed that the intensity of light in this region was not great. A period of from ten to forty-five minutes was allowed for each orientation. Although the influence of the light tended to drive the lobsters off the sanded area the results of six trials (ten lobster each) showed that thirty-seven fifth-stage lobsters remained in contact with the sand, while twenty-three moved to the clear area.

Case 3—In the next series of six trials (ten lobsters each) the intensity of light was modified by substituting an orange glass before the end window. The results showed twenty-five on the sanded area, thirty-five on the clear.

Case 4—In the last series of six trials (ten lobsters in each) the conditions were still further modified by removing the orange glass and thereby greatly increasing the intensity of the light which entered the end window of the box. This demonstrated that a light of great intensity would drive the fifth-stage lobsters off the sanded area. At the end of the experiment only thirteen lobsters remained on the sanded area, while forty-seven remained in the clear region. Finally, the sand was removed from the box, and the reaction of these lobsters was tested with unobstructed light

entering the end window. The resulting reaction was invariably and definitely negative; and this with light of all the intensities used in the previous cases.

Conclusions from experiments on contact-irritability versus reaction to light—Although these experiments can hardly be called critical, they demonstrate that the presence of the sanded area in the box did modify the reactions of the fifth-stage lobster. That there was manifested a tendency to remain in contact with the sand, to burrow in it, and not to be dislodged by such intensities of light as would normally rout the entire group of lobsters and send them to the end of the box farthest from the light. These facts, moreover, cannot be said to hold true for the fourth-stage lobsters that were used in the foregoing experiments, and which showed no well defined preference for the sanded area, at least in the early part of the stage-period.

VI. MECHANICS OF ORIENTATION.

The aim of the present section is to report the results of a series of observations which were made in order to answer the following question: By what movements of the lobster larvæ are the reactions to light accomplished? In our effort to answer this question we shall, for the present, attempt to avoid so far as possible considerations which deal directly with the ultimate causes of orientation; in other words, we shall limit ourselves to the observation of the actual movement of the body, or of certain parts of the body, of individual larvæ; and attempt to show what relation exists between these movements and the external factors which appear to determine them. First, however, it is necessary to establish some points regarding the natural behavior of the larvæ when the influence of external stimuli is at the minimum.

1. *The normal behavior of the larvæ*—In view of the fact that swimming constitutes the chief activity of the larval lobsters, our question resolves itself into the following: What is the nature of the normal swimming? When one first observes the behavior of individual larvæ amidst the thousands contained in the large hatching bags no difference is evident in the swimming of the first three stages. In all instances the back of the larva is, for the most part, uppermost, the abdomen bent under and downward at an angle of about 60° from the longitudinal axis of the cephalo-

thorax, which in turn is inclined about 30° from the horizontal plane. In daylight this position may be maintained without modification for several minutes, but the equilibrium is often interrupted by other body-movements which, upon superficial examination, appear to be of a most diverse and ill-ordered nature. There are leanings, turnings, fallings, somersaults, revolutions and rotations which follow each other in no apparently definite sequence, and which disturb the general equilibrium greatly or slightly as the case may be.

Whether the balanced equilibrium, the devious rotations or other activities are present, the exopodites or swimming attachments of the thoracic appendages beat the water more or less constantly with short vibratory strokes, sometimes lifting the larvæ high toward the surface, and again allowing them to sink to the bottom, where they frequently lie for some moments almost motionless, only again to resume their varied activity. Now they swim forward, now backward, now lurch to the side, now to the rear, always maintaining more or less energetically these apparently aimless movements. Such is the nature of the swimming in daylight or other brilliant illumination; but for our purpose it cannot be called the normal swimming of the lobster larvæ. It is only under special conditions that the latter may be observed; and, in view of the fact that it is the conditions of light which influence more strongly than any other factors the behavior of the larvæ, it is only when they are under certain light-conditions that we may expect to find manifested what we may call the characteristic or normal swimming.

The twilight or nocturnal swimming of the larval lobsters invariably gives us the fairest example of natural behavior. At such times alone (or when the larvæ are submitted to artificially produced twilight) variations in temperature and the multiplicity of conflicting cross-light influences are eliminated. Frequently when the twilight was so dim that observation was rendered difficult, the swimming was delicate and regular, and the young larvæ would mount up, bird-like, to the surface of the water, hover many seconds in a single position, or swim backward or forward with equal ease. In such a case, when a lighted match was brought near the side of the jar in which the larvæ were confined, the same restless and uncertain swimming, characteristic of the diurnal activities, was again manifested, together with the accompanying leanings and

rotations. From these facts it may be assumed that the twilight swimming of the larvæ probably represents the natural behavior or at least the behavior that arises purely from the internal states themselves; and that the peculiar antics characteristic of the daylight swimming represent a type of behavior chiefly due to the action of external stimuli.

The question now naturally arises—Do the various turnings, rotations, leanings, and fallings which constitute the apparently haphazard behavior of the larval lobsters when swimming in daylight or other brilliant illumination, give any indication of method? Observations have given a suggestion as to the means whereby we may attempt to ascertain the value of certain light-conditions in determining these peculiar forms of behavior.⁵

If larval lobsters of any of the first three stages are subjected to the influence of light which comes from one direction only, as from the side, the first fact observable is that the larvæ undergo a certain body-orientation; they turn away from the light and place the long axis of the body parallel to the direction of the rays. The second fact which may be noticed is that the larvæ move in the direction of the light rays either toward or from the source of illumination. A third fact, which is of prime importance and which involves those stated above, is that no matter whether the progressive movement of the larvæ be toward or away from the source of light, the orientation of the body (head away from the source of light) remains unchanged. To state the matter briefly we may say that, whatever the nature of the progressive orientation of the larvæ, *the body-orientation is at all times, and under all conditions, negative*. BOHN (1905, p. 8) has clearly pointed out this fact for the larvæ of the European lobster. In this regard he says: "En général, les larves de homard se placent dans le sens négatif; même, dans les premières heures après l'éclosion, alors qu'elles se groupent vis-à-vis des lampes, leur tête se tourne du côté opposé, et les larves s'approchent de la lumière en regardant l'obscurité, c'est-à-dire en reculant. Ainsi, après l'éclosion, l'orientation a lieu dans le sens négatif, mais le déplacement se fait dans le sens positif. Dans la suite, si le sens de l'orientation

⁵ Many of the observations which follow were made previous to the writer's knowledge of the excellent work of GEORGES BOHN (1905) along similar lines, upon the larvæ of the European lobster, *Homarus vulgaris*. The writer would acknowledge, however, his great indebtedness to this investigator, whose work has proved suggestive in the highest degree, and whose observations on the mechanics of behavior the writer has been able, in the majority of instances, to verify as well as supplement.

reste le même, le sens du déplacement peut changer." LYON (1906) has recorded a similar observation for several larval stages of Palemon. This condition of affairs is rather at variance with the majority of observations on the phototactic reactions of animals and it is contrary to the condition of body-orientation which we find in the fourth stage of the lobster itself, for in this stage (at least in some of the assumed phototactic reactions) the body-orientation brings the head toward the source of illumination instead of away from it as is invariably the case in the first three stages.

The question has already arisen as to what we may mean by a positive phototactic reaction, for in this case it is clear that we may very frequently have a negative body-orientation coupled with a positive progressive orientation. Until we know more regarding the differences between body-orientation and progressive orientation, it may be considered safe to say that the *direction of the progressive movement*, with respect to the source of illumination, may be held as the surest criterion of the sign of the phototactic response of animals. On the other hand the point has been made clear by some writers, that in the body-orientation of organisms the definite relation of the body-axis to the lines of active force is the primary consideration for all problems of progressive orientation. However this may be, we have before us at least one instance wherein, although the relation of the body-axis to the lines of force is an important consideration, the body-orientation *per se* has little or nothing to do with the question of the positive or negative progressive orientation of the organism; for as we have already observed, conditions which invariably determine a negative body-orientation may determine either a positive or a negative progressive orientation, as other circumstances demand. We may, therefore, first concern ourselves with the *mechanics of progressive orientation* and then turn with better understanding to the *mechanics of body-orientation*, for these two reactions apparently depend upon quite different circumstances.

2. *The mechanics of progressive orientation*—The only means of locomotion possessed by the larvæ of the first three stages are the exopodites of the thoracic appendages and the strong, flexible abdomen with its broad terminal fan (Fig. 1). It is but seldom, however, that the latter is used, and never when it is a question of progressive orientation to light. We are then confronted with the problem: How, by the motion of the thoracic exopodites

alone, is the larval lobster able to execute those movements which determine his progress either toward the source of illumination or away from it?

If the larval lobsters in any of the first three stages be put in a glass jar which is surrounded by black paper and placed in subdued daylight, the short vibratory strokes of the exopodites can be readily observed. At one time, certain individuals may be seen to swim rapidly backward, and again forward, with no apparent change in the position of the body or in the direction of the stroke of the exopodites. If, however, the thoracic appendages themselves be carefully watched, one can observe that, from time to time, these limbs undergo either a forward shifting (extension) as shown in Fig. 8, or a backward shifting (contraction) as shown in Fig. 9. This change from the "anterior" position to the "pos-



FIG. 8.

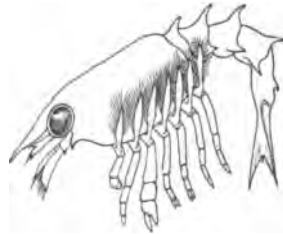


FIG. 9.

FIG. 8 shows a larval lobster with the thoracic appendages in the extended or "anterior" position; the resulting movement is forward and upward.

FIG. 9 represents the appendages in the contracted or "posterior" position; the resulting movement is backward and upward.

terior" position may occur at short intervals, each position may persist for some seconds, or there may be a successive alteration with periods of longer duration in either one position or the other. It may be observed further, that when the thoracic appendages take the "anterior" position, the direction of the strokes of the exopodites becomes somewhat forward as well as downward, and the *resulting motion of the larvæ becomes backward and upward*. When, on the other hand, the thoracic appendages assume the "posterior" position, the stroke of the exopodites becomes backward and downward; and the *resulting motion of the larvæ becomes forward and upward*. During a great part of the time, the upward movement of the larvæ, as a result of the outward and downward stroke of the exopodites, does little more than compensate for the natural tendency to sink toward the bottom. For this reason the

progress of the larvæ may often be directly forward or directly backward with but slight deviation from the horizontal plane; while at other times, when the stroke of the exopodites is directly outward and downward (exclusive of either the "forward" or "backward" factor), the larvæ may mount to the surface in nearly vertical lines.

It thus becomes evident that the progression of the larvæ, backward or forward, upward or downward, is largely determined by the position (state of extension or contraction) of the thoracic appendages. In other words, if for the greater part of the time these appendages are in the "anterior" position the phototactic reaction of the larva is positive; but on the contrary, if the thoracic appendages are more frequently in the "posterior" position, then the consequent reaction of the larvæ is negative. Naturally the next important question which arises is: What conditions determine the "anterior" or the "posterior" position of the thoracic appendages? It cannot be questioned that these changes are directly due to certain variations in the intensity of the illumination and are modified by the "physiological state" of the larvæ themselves; and that, furthermore, the state of extension or contraction of the thoracic appendages, and the stroke of the exopodites, are regulated to a great degree through the mediation of the eyes and the nervous system of the larvæ. But further consideration of this subject must be postponed until later. In the meantime we may turn our attention to the mechanics of body-orientation.

3. *The mechanics of body-orientation*—Under the present heading we shall consider the nature of those peculiar movements which the lobster larvæ undergo when they are under diverse and changing conditions of stimulation, in order to explain the cause of these actions and to show their relation to certain definite laws which may be said to regulate to a great degree the body-orientation of the larvæ. As we have observed, it is the influence of light which is most active in determining the behavior of the larvæ; furthermore, it is in the absence of such influences as diverse and changing conditions of illumination afford that the most realistic picture of the normal behavior of the larvæ is obtained. It will then prove the most practical method of approaching this problem, first, to obtain conditions of light which allow natural behavior (normal swimming); and then, by gradually modifying these conditions, to observe the effects upon the behavior of the larvæ.

A. THE EFFECTS OF DIRECT LIGHTING AND SHADING. *Technique and Methods of Observation*—This section deals more especially with the directive influence of light rays so introduced as to strike the larvæ from different directions; from before, from behind, from the side, from above, from below, or obliquely to the body-axis. These conditions were obtained, for the most part, in two ways. The larvæ were placed either in a cylindrical glass jar, or in an especially constructed rectangular glass box (similar, perhaps, to the *révélateur* used by BOHN), three inches wide, six inches long, and two and a half inches deep, all sides and the bottom being of glass. Either of these receptacles might be placed in the dark box already described. To regulate the intensity, slides of colored glass were used as in the earlier experiments,

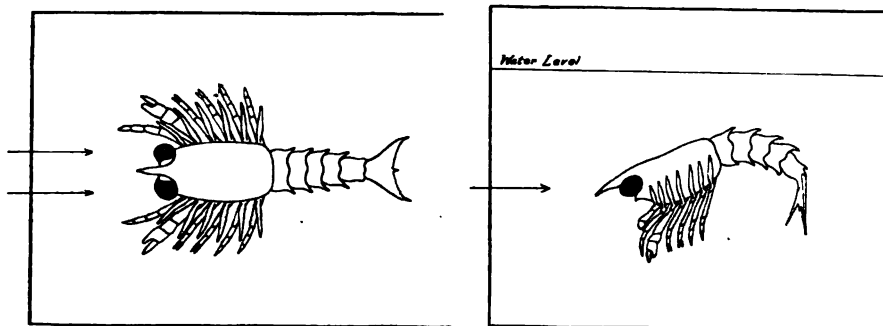


FIG. 10.

FIG. 11.

FIG. 10 represents a dorsal view, FIG. 11 a lateral view, of a larval lobster in the glass container. For description, see Case 1, p. 265.

while to change the direction of the rays a series of mirrors was employed. In certain instances, when light from the bottom was required, the receptacle containing the larvæ was placed upon a glass plate raised a certain distance above the bottom of the box, and the mirror was placed below. In still other instances the direction or the intensity of the light was modified by the use of light-absorbing (black) or light-scattering (white) backgrounds. These were used more frequently when the observations were made in diffuse daylight, and the subdued light came to the glass containers from several different directions. From the experiments it appears very probable that in determining the orientation of the organisms, the backgrounds were instrumental only in regulat-

ing the amount and the general direction of the light which they reflected or absorbed. First, however, we shall consider the effects of suddenly throwing the light from a certain direction upon larvæ oriented in various positions.

Case 1. Illumination from before—In the first instance the behavior of a single larva was studied (the stage does not matter). It was oriented in the rectangular container, in the dark box with its head toward the three by one inch window, which was closed (Fig. 10), but in such relation to the glass box that its longitudinal axis was parallel to the direction of the rays of light coming from this window when it was opened! While the larva was so oriented, the screen was drawn aside and light from the small window was allowed to strike the larva "head-on." Under these conditions, one of two reactions resulted. The larva underwent either a forward or a backward somersault, or rotation, which brought the back below with the head directed away from the source of illumination. Whether the rotation was backward or forward made no difference in the resulting orientation and which one occurred depended upon the direction of the rays of light which struck the eyes of the larva. In normal swimming the body of the larva in any of the first three stages is bent about 30° from the horizontal. Now if the rays of light had the direction of *A* or *B* (Fig. 12) the rotation was usually forward, while if the light came from below, direction *C*, the rotation often was backward. After this first orientation the larva (position *B'*) frequently performed a rotation on its long axis, either to the left or right, which brought the back again uppermost, and it then progressed in the direction of the rays, either toward or away from the source of illumination.

Corollary 1—If the rays striking the eyes of the larva had the slightly oblique direction shown in Fig. 13, *a* or *c*, but were in direction or plane *B* (Fig. 12), then the larva pivoted at the middle of its own longitudinal axis and swung to one side or the other, always keeping the back uppermost.

If the rays of light took the direction designated $a^1 - a^4$ or $c^1 - c^4$, the result was the same; the larva swung until the longitudinal body-axis was parallel with the incident rays, and the head was directed away from the source of illumination.

Corollary 2—If the rays striking the eyes of the larva had the oblique direction, $a^1 - a^4$ or $c^1 - c^4$ (Fig. 13) in plane *A* of Fig. 12, then the resulting movement was a combination of the forward

rotation and the side swing (Cor. 1). In other words, the larva performed a side-somersault, and ended with the back directed below and to the side. Whether it turned to the left or to the right depended upon the direction of the rays in either the *a* or the *c* series. At the end of this reaction the larva usually became righted again with the back above and the head away from the light, and continued its progressive orientation in one direction or the other according as the reaction was positive or negative.

Corollary 3—If the rays striking the eyes of the larva had the oblique direction $a^1 - a^4$ or $c^1 - c^4$, and were in plane *C* of Fig. 12, the resulting reaction was a combination of the backward rota-

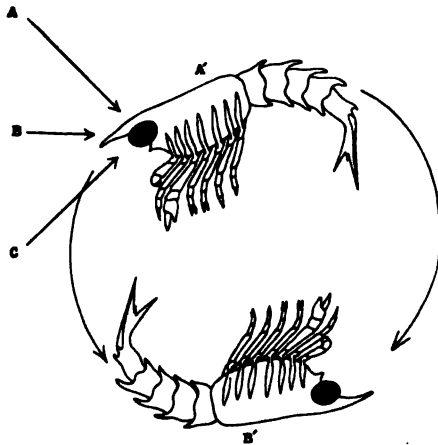


FIG. 12. For description, see Case 1, Cor. 1.

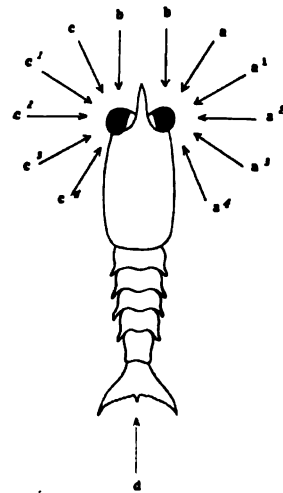


FIG. 13. For description see Case 1, Cor. 2.

tion and the side swing (Cor. 1). That is to say, the larva performed a backward side-somersault, became oriented as in Corollary 1 and 2, again turned the back uppermost, with the eyes directed away from the source of light, and continued its progressive orientation, in one sense or the other.

Case 2. Larva lying with back downward; head toward light—In these instances, the larva was oriented head toward the (closed) window, and back downward. The rays were introduced from before, as in Case 1. It may be said that this orientation was difficult to obtain. Often it was necessary to wait fifteen minutes

or more before it occurred, then at the proper moment the light was admitted and the consequent reaction observed. On the other hand, it was common to find the larvæ on their backs and oriented obliquely to the rays of light. When the larva was oriented in this manner and the light was admitted, there usually occurred either a forward or a backward rotation (Fig. 14), but the forward rotation was most common. Whichever one occurred, however, the final orientation was the same: the back of the larva was again brought uppermost, and the head was directed away from the source of light.

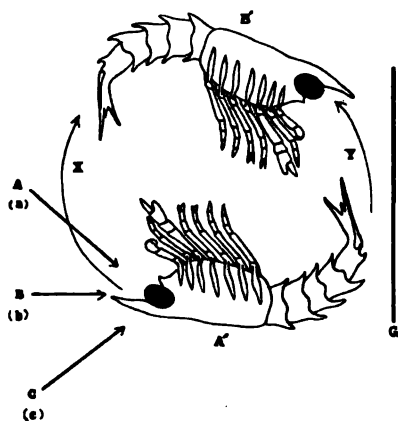


FIG. 14. For description, see Case 2.

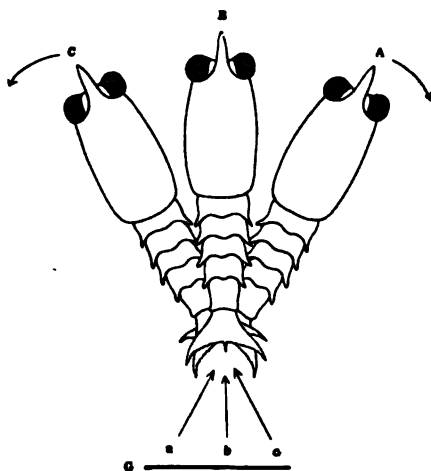


FIG. 15. For description, see Case 4.

Corollary I—If the larva was oriented with the back below, the head toward the closed window, and the body-axis oblique to the direction of the incident rays, the resulting orientation was a combination of the upward and forward rotation and a swing of the body, pivoted on the middle of its long axis, away from the incident rays (this last reaction was similar to Case 1, Cor. 1, except that in the former instance the larva oriented back below). The final orientation was as in Case 2 (Fig. 14, B'). Whether the incident rays were in plane A, B, or C did not appear to make as much difference in the manner of orientation when the lobster was lying back below. It was observed that rays coming from above (plane A) more frequently determined the backward rota-

tion; and that rays coming from below (plane *C*) more often determined a forward rotation.

Case 3. Larva lying with the side downward; head toward light—In this case, the larva was oriented with one side uppermost and the head turned toward the source of light. The conditions may be represented by Fig. 14, if it be imagined that for the present case the larvæ are lying in a horizontal plane rather than in the vertical as originally intended in this figure. The arrows *A*, *B* and *C* represent rays in the same vertical plane, while (*a*), (*b*) and (*c*) represent them in a horizontal plane. When the light was admitted to a larva so oriented, the reaction was similar to that described under Case 2. In the present instance, however, when the rays had the direction (*a*), the backward rotation was more likely to occur than when the rays had the direction *A* as in Case 2. Rays in the direction (*b*) or (*c*) almost invariably determined a forward rotation, in which, if the larva was fatigued, it would merely turn through 180° in the same plane, and become oriented, still lying on the side, but with its head away from the source of light. If, however, the larva was fresh and active at the end of the rotation of 180° in the arc of a circle (*A'*), it would rotate through 90° on its longitudinal axis and come into the normal swimming position with the back uppermost and the head directed away from the source of light.

Case 4. Larva oriented with back above; head directed away from the source of light—When the larva was thus oriented and the light was so introduced that the rays streamed in a direction parallel to the longitudinal axis of the larva, no change in the body-orientation took place. The progressive orientation, however, might continue as either positive or negative. In case, however, the light came from the sides *a* or *c* (Fig. 15) the larva reacted by swinging (pivoted on the middle or end of its longitudinal axis) to either one side or the other, and it might then undergo positive or negative progressive orientation. If the direction of the rays changed through the series, *a*, *b*, *c*, the larva could likewise be made to swing as regularly as a pendulum and for long periods of time, according as the light came from one side or the other. Indeed the animal was quite at the mercy of the influence of light.

In case the light came somewhat from above as shown in Fig. 16, *A*, the larva would incline itself farther forward, the number of degrees of rotation depending upon the degree of the angle.

formed by *A* with the horizontal. When the angle was slight the forward rotation of the larva was but a few degrees, and it continued to swim in this body-position, and might undergo a positive or negative progressive orientation, as ordinarily. When, however, the angle between *A* and the horizontal was greater, the degree of rotation of the larva was proportionately greater, and in certain cases it might undergo a rotation of 180° and fall to the bottom.

When, on the other hand, the incident rays struck the larva in the direction of *C* (Fig. 16), then the larva underwent a backward rotation whose degree was dependent upon the breadth of the

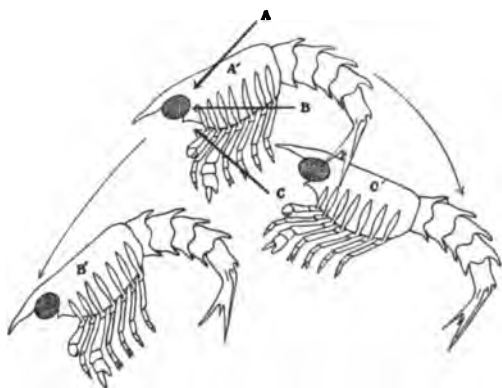


FIG. 16. For description, see Case 4.

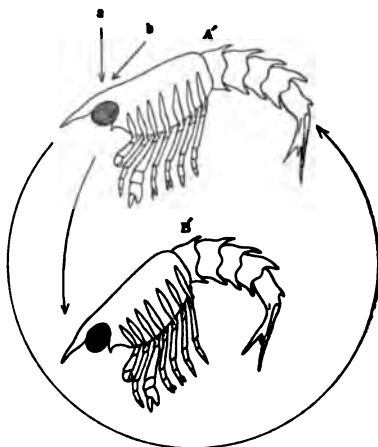


FIG. 17. For description, see Case 6.

angle between *C* and the horizontal. If the angle thus formed was slight, the backward rotation of the larva was correspondingly slight, and it would continue to swim in the position designated *C* (Fig. 16), undergoing positive or negative progressive orientation as other conditions of light might determine. If the angle formed between *C* and the horizontal was great, the degree of backward rotation of the larva was proportionately greater, and a fall to the bottom, tail downward, might result.

Corollary 1—When the direction of the rays was determined by compounding the vertical series of light factors (*A*, *B*, *C*, Fig. 12) with the horizontal series (*a*, *b*, *c*, Fig. 15), the resulting reaction was a combination of the two types of behavior described above.

Case 5. Larva oriented with back above and longitudinal body-axis at right angles to direction of light rays—When the larva was oriented as above and the rays were introduced at right angles to the longitudinal axis (Fig. 13, *a*², *c*²) the behavior was similar to some phases of Case 1, Cor. 1. The larva swung directly away from the source of light until its longitudinal axis was parallel to the light rays, with the head directed away from the source of light. Obviously the swing might cover from 1° to 90° and either positive or negative progressive orientation might follow.

If the larva was lying with the back below, but otherwise oriented as in the previous instance to the directive influence of the rays, the reaction was the same; namely, a swing to one side. This resulted in placing the longitudinal axis parallel to the rays of light. Frequently, in such case, the larva would undergo a rotation on its own axis, so that it assumed a position with the back uppermost and the head directed away from the source of light. Whether or not this "righting reaction" occurred, appeared to depend largely upon the degree of freshness. Individuals which had undergone fatigue more frequently refused to rise from the bottom. It was at no time possible, however, to fatigue the larvæ to such an extent that they would not give the "swinging-reaction" into line with the light rays. By alternately changing through an arc of 30° the direction of the light which struck the larvæ from behind (Fig. 15, *a*, *b*, *c*), they could be made to swing, pivoted on the middle or end of their longitudinal axis, in an arc of equal degree. This pendulum-like activity in answer to the change in direction of the light-stimulus was extremely constant and in no case was it observable that the reaction was diminished by fatigue in spite of long periods of such alternate directive stimulation. It may be added here that prolonged direct stimulation from behind never produced a change in the body-orientation of the larva. The progressive orientation, however, might take place in either the positive or the negative sense.

Case 6. Larva oriented with back above; light enters from above—Under the conditions mentioned above, the larva was forced to give one or two reactions, depending upon the degree of intensity and the suddenness of introduction of the light:

(1) In some instances (especially when the light had the direction, *b*, Fig. 17), the larva first rotated through an arc of greater or less curvature and finally assumed a new swimming position

with the longitudinal axis of the body bent at a greater angle from the horizontal plane (Fig. 17, *B'*). This new swimming position was usually maintained so long as the conditions of light remained the same, but was sometimes replaced by the second form of reaction, which usually occurred when the light had the direction *a*, and which was merely an exaggerated form of the first.

(2) In this second type of reaction the rotation of the larvæ was not limited to an arc of a few degrees, but was extended into a forward "somersault." This in turn took place in one of two ways: (*a*) the larva might accomplish a rotation of 360° and return to its original position with the back above, but since the stimulation from above remained the same, it would not rest in this position, but would continue for a time to perform complete rotations without pause, after which it would come to rest as shown in Fig. 17, *B'*. This new swimming position was sometimes maintained as long as the conditions of light remained unchanged, though it might give place to further rotations; (*b*) the larva might, as a result of the forward rotation, come to rest with the back directed below, but this orientation was only momentary, because the influence of the light from above immediately determined a backward rotation. This last reaction might culminate when the larva had gained the new position shown in Fig. 9, *B'*, or it might be continued into one or more backward rotations through 360° and culminate after a greater or less number of such rotations, by coming into the new swimming position mentioned above. This orientation would be maintained as long as the same conditions of light were in effect; or it might be interrupted from time to time by rotations in arcs of varying degrees, and in either of the directions mentioned above.

Corollary 1—If, when the larva was oriented as in Case 6, the light was introduced from both sides and above, the resulting reaction was a combination of the forward rotation and the side swing. If the light came from above and behind (Fig. 17, *b*), then the direct assumption of the new swimming position *B'* more frequently resulted without the variable number of rotations through 180° or 360° .

Case 7. Larva oriented with back below; light enters from above—Under the above conditions of orientation (Fig. 18) there was usually one constant form of reaction. The larva would undergo a backward rotation through about 120° , and come into a new

swimming position with the axis of the body bent downward several degrees from the normal swimming position (perhaps 45° from the horizontal), the exact amount appearing to be dependent upon the intensity of the light. This new swimming position was usually maintained as long as the conditions of light remained unchanged. It might sometimes be interrupted by backward rotations through 360° . These rotations invariably culminated in the assumption of the new swimming position (Fig. 18, *B*). In case the direction of the rays was both from the side and from above the resultant reaction was a combination of the reaction described above and the direct side swing.

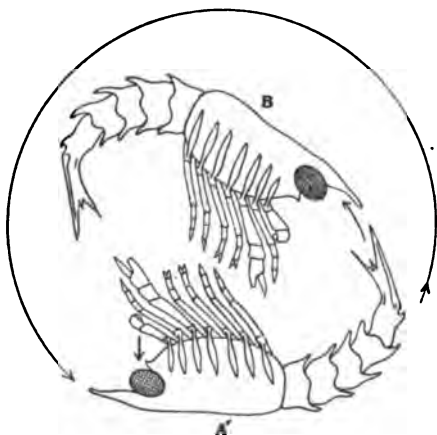


FIG. 18. For description, see Case 7.

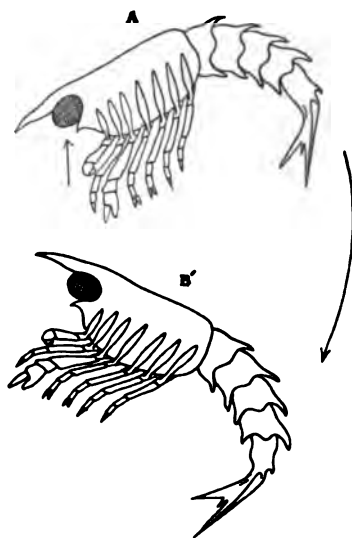


FIG. 19. For description, see Case 8.

Case 8. Larva oriented with back above; light enters from below—Under these conditions of orientation, the nature of the reaction was similar to that described in Case 6. Usually there resulted a direct backward rotation through a few degrees, which produced a new swimming position, Fig. 19, *B'*. This was usually constant while the conditions of light remained the same, but it was sometimes interrupted by backward rotations through an arc of greater extent, or even by a variable number of complete backward rotations through 360° . At the end of these, however, the new swimming position *B'* was invariably assumed. Combinations of the

directions of the light (as both from the side and from above) produced modification in the reaction, but these could at any time be predicted if the individual constituents of the light were known.

Case 9. Larva oriented with back below; light enters from below—Under the conditions of orientation stated above the resulting reaction was similar to that described under Cases 6 and 8, but reversed. As in these instances, one of two results usually occurred: (1) The larva would undergo a forward rotation through a variable number of degrees, and assume directly a new "swimming-position" as shown in Fig. 20, *B'*. It was readily observed that the head was directed upward and away from the

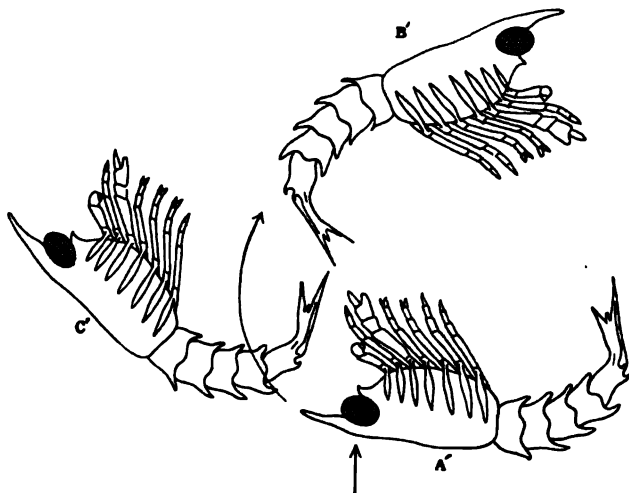


FIG. 20. For description, see Case 9.

light, not downward at an angle of about 30° from the horizontal, as in the normal swimming position; (2) it might happen, however, that instead of assuming this orientation the larva would merely come to an orientation with the back below and with the head directed upward as a slight angle as shown in Fig. 20, *C'*. It might, again, undergo one or more complete rotations forward, through 360° and then assume the new position shown in Fig. 20, *B'*, which position might be retained as long as the light conditions remained unchanged. The definiteness in these two reactions could be modified, as a result of changing slightly the direction of the light.

In addition to the facts regarding the effect of direct lighting upon body-orientation, which have been presented in the form of these nine cases, several other conditions might be mentioned:

1. If the longitudinal axis of the larva was parallel to the direction of the incident light rays, and the head away from the light, then the introduction of light produced no change in the body-orientation, but it might cause a positive or a negative progressive orientation.

2. In order that the unmodified forward or backward rotation might occur, it was learned that the light rays must strike both eyes with equal intensity, and consequently in a direction exactly perpendicular to any transverse body-axis of the larva.

3. In case the incident rays came from a direction that was not exactly perpendicular to the transverse axis of the larva, be the angle of difference ever so slight, the perfect backward and forward rotation would not occur, but would be greatly modified by swingings of, and revolutions on, the longitudinal axis of the body.

4. This type of behavior could not be observed unless the conditions of light were reduced to a single directive influence, and this factor handled with very great precision.

The effect of blocking the illumination—In the previous section we have examined the reactions which were brought about by suddenly introducing rays of light in directions which maintained a certain definite and specified relation to the longitudinal or transverse axis of the larval lobsters. In the present instance, however, we are to consider the nature of the reactions which are produced as a result of suddenly excluding or blocking the principal source of light by which the larvæ have just previously been stimulated. The "cut-off" was made by closing the window through which the light came, and thus leaving the larvæ in the subdued and diffuse light which entered the dark box from the room. Since the body-orientation of the larvæ to the directive influence of the light is always the same, obviously there could not be many different varieties of orientation caused by the change in the conditions of light. Such as were possible, however, may be described as follows:

Case 10. Larva oriented with the back above and the longitudinal body-axis exactly parallel to the incident rays—In case the larva was oriented as described above, when the light was shut off

there usually resulted a forward rotation through 180° . This reaction caused the larva to become oriented (often on the bottom) with the back below and the head toward the previously existing source of light. This position was not maintained, but was succeeded by a "righting reaction," usually a revolution on the longitudinal axis, which brought the back again uppermost. After this response the larva might swim in diverse directions.

Case 11. Larva oriented with the back above and the head away from the light, which comes slightly from the side—If, when the larva was oriented as described above, the light was suddenly cut off, there resulted a swing of the long body-axis so that the larva was brought more or less nearly to face in the opposite direction; i. e., in the direction from which the light had previously come. This orientation, however, was not permanent, but other consequent reactions occurred and the larva might swim in one of several directions.

Case 12. Larva oriented as in Fig. 17, B'—If the direction of the light was from above, and the orientation of the larvæ as in Fig. 17, B', when the light was cut off, the head of the larvæ would swing upward to face the direction from which the rays had previously come. Consequently, however, the orientation became that of the normal swimming position.

Case 13. Larva oriented as in Fig. 20, B'—When, as the result of light stimulation from below (as in Case 9), the larva was oriented with the head directed upward, and the illumination was suddenly cut off, the head of the larva would swing downward to face the direction from which the light had previously come; sometimes the larva would perform a rotation in an arc of greater or less extent and fall to the bottom. The body-orientation with head downward was not maintained, however, but was at once superseded by the normal swimming position.

It thus appears from these cases that there was usually an excessive movement to produce the new body-orientation; but that these movements invariably ended in the assumption of the normal swimming position.

Résumé of experiments on the effects of direct lighting and shading—(A) The effect of suddenly submitting the larval lobsters to a light which has a directive influence is to cause the larvæ to orient themselves in such a manner that the longitudinal axis of the body finally assumes a definite relation to the direction of the

light rays. This orientation is a position with the long axis of the body parallel to the light rays, and with the head turned away from the source of light. (B) The effect of suddenly blocking the light to which the larvæ are reacting phototactically is to cause a new body-orientation by which the head is usually brought to face the direction from which the light had previously come. In either of the cases mentioned above the body-orientation is brought about by a single motor reflex or by a longer or shorter series of motor reflexes, some of which are "over-produced" movements.

These movements include the following types:

1. *Forward or backward rotations,⁶ or somersaults*—These were rotations in an arc, of a few degrees, which directly determined a new swimming position with the head raised or lowered, depending upon the direction from which the light or shadow had been introduced. In other cases these rotations took the form of a variable number of complete rotations through 360°, either backward or forward, in which the body of the larva formed a constant part of the circumference.

2. *Revolutions on the longitudinal axis of the body or rollings*—The revolutions or rollings took place either to the right or left, but usually in such direction that the back of the larva became directed more or less toward the light. They might be through a few degrees, or they might exceed 90°, in which case the larva fell to the bottom. In the case of larvæ one of whose eyes had been injured this revolution took place very rapidly, oftne at the rate of one hundred and fifty per minute, and always in a determined direction, the normal eye over, the injured eye under (HADLEY 1907b).

3. *Swingings of the longitudinal axis of the body*—These reactions were swingings in such a direction that the head was brought by the shortest path to face the dark, and the tail to point toward the light.

⁶Three similar types of movement are described by BOHN (1905, p. 4) as follows:

- 1° *Mouvement de manège*—l'animal décrit un cercle de plus ou moins grand rayon, l'axe du corps, courbé en arc, faisant partie constamment de la circonférence; la rotation se fait tantôt dans le sens des aiguilles d'une montre, tantôt dans le sens inverse. Parfois, au lieu de décrire un mouvement de manège pur, l'animal décrit des courbes de rayon variable qui constituent une sorte de spirale.

- 2° *Mouvement de rotation en rayon de roue*—l'axe du corps ne dévie pas; il est une des parties d'un des rayons du cercle décrit, et non une partie de la circonférence du cercle: la tête peut se trouver à la circonférence ou au centre.

- 3° *Mouvement de rotation sur l'axe, ou roulement*: l'animal tourne autour d'un axe longitudinal qui traverserait le corps dans sa longueur; la rotation commence par une inclinaison de l'animal d'un côté, et le sens de la rotation se trouve ainsi déterminé. Le roulement peut s'accompagner d'un mouvement de translation et devient un mouvement en pas de vis.

4. *Rotations in the radii of a circle*—In these the longitudinal axis of the larva formed a radius, and with either the head or the tail at the center the animal rotated about a fixed point. These reactions were uncommon and, as yet, unexplained.

These four types of movement seldom occurred separately, except under especially devised experimental conditions. Under natural conditions, they were usually combined to form a composite action. To the previously mentioned simple components, however, all the more complex movements of the larval lobsters could be reduced.

B. THE EFFECT OF SCREENS AND BACKGROUNDS—It is probable that the reactions which are brought about through the use of backgrounds, are, generally speaking, dependent upon the same factors and conditions of illumination which are effective when light-absorbing or light-scattering screens are used. The term "screening" has been employed by BOHN (1905) to designate his method of submitting organisms to the influence of surfaces of light and shade. This investigator made use of screens of black and white of such size that he could readily bring them close to the sides of the glass containers in which the organisms under observation were placed. He has made a special study of the reactions of Crustacea to the influence of such screens, and in several instances the observations of the writer upon the larvæ of *Homarus americanus* merely confirm certain points in BOHN's earlier work. In many instances, however, new facts have been added.

The influence of white screens—The lobster larvæ were confined in a cylindrical jar, crystallization dishes, or in a rectangular glass container. The latter was used most frequently. The larvæ were then placed in the dark box and this was illuminated in such a manner that a general twilight was produced and the directive influence of light was at a minimum. While making observations it was even found necessary that the writer should wear a black mask over his face and collar, and, often, darken his hands in order not to modify the uniform light. For white screens pieces of white cardboard were employed, and brought over, under, or beside the receptacle containing the larvæ, as the case might require. Sometimes the screen was brought gradually toward the container, sometimes abruptly; but in all cases the results were definite and agreed with great uniformity. In order to secure the best results with the white screen, it was found best to reduce the

intensity of light within the dark box below the degree used in the case of the black screens. The results of the series of experiments with white screens may be summarized as follows:

Case 14—When the larva was oriented with back above and the screen, held vertically, was so introduced from before that its plane was at right angles to the longitudinal axis, and parallel to any transverse axis of the larva, there resulted a rotation through 180° with, perhaps, a fall to the bottom. After this, and as a result of a revolution on the body-axis, a "righting reaction" usually occurred and the back would again be brought above. Now, with the head directed away from the white screen, the larva might either approach or depart from it, according as the progressive orientation was positive or negative. Sometimes, instead of producing a rotation through an arc of 180° , the larva underwent a series of rotations, its body forming a constant part of the circumference. The final orientation mentioned above would, however, invariably succeed. In case the screen was not held squarely before the larva, but somewhat at an angle to any transverse axis, the consequent reaction was a direct side swing away from the screen in order to place the longitudinal body-axis perpendicular to, and the head away from, the screen. In other cases there resulted a combination of the side swing and the forward rotation, so that the larva performed a sort of "half-somersault," and eventually assumed the normal swimming position, with the head directed away from the screen, as pointed out above.

Case 15—When the larva was oriented with the back above and the screen, held vertically, was made to approach the posterior end of the larva, no change in the body-orientation resulted. There might occur, however, either a positive or a negative progressive orientation.

Case 16—In this case the larvæ were swimming promiscuously about the container. When the screen was made to approach larvæ which held a position with the back above and one side turned toward the screen, these larvæ experienced a swing of their longitudinal axis so that the head came to be directed away from the screen and the longitudinal body-axis at right angles to the plane of the screen.

Case 17—When the screen, held horizontally, was made to approach, from below, a larva which held the normal swimming position, one of two reactions (which probably represent different

degrees of the same reaction) resulted: (1) The larva would swing the head upward as shown in Fig. 20, *B'*, and maintain this swimming position so long as the light condition remained unchanged, or (2) it might, on the other hand, experience this same reaction in an exaggerated form, i. e., there might result a backward rotation through 180° , which reaction would cause the larva to fall to the bottom and to assume a position with the back below and with the head directed upward at a slight angle as shown in Fig. 20, *C'*. Usually, however, this form of orientation resulted only when the light was of greater intensity, such as that secured in cases of direct illumination.

Case 18—When the larva was oriented in the normal swimming position and the white screen was made to approach from above, the reaction was similar to that described for Case 6, p. 270. The one difference was that while the direct lighting often caused a number of complete rotations through 360° before the final body-orientation was assumed, the white screen, on the other hand, usually acted by changing the swimming position directly to that of Fig. 17, *B'*. This difference in response was probably due to the difference in the intensity of light (direct or reflected) coming from above.

The black screen—The method of conducting the experiments with the black screen was almost the same as that for the white screen. There was one point of difference. It was found that, in order that the black screen should determine any reaction of the larvæ, it was necessary to have a slightly greater illumination within the dark box. The following report of cases shows the result of making the screen to approach, from various directions, the larvæ diversely oriented.

Case 19—When the larva was in the normal swimming position and the back screen was presented opposite the head, and at right angles to the longitudinal axis, the orientation was not changed, but was retained constantly so long as the screen remained in position.

Case 20—When the larva was in the normal swimming position and the screen was made to approach from behind, so that its plane was parallel to a vertical plane passing through both eyes of the larva, there usually resulted a forward rotation of 180° in the arc of a circle. This reaction brought the back of the larva below, and the head toward the black screen. This position was

at once further modified by a revolution of 160° on the long body-axis, either to the left or right (determined by the nature of the lateral or secondary illumination), and the larva again assumed the normal swimming position, but with the head directed toward the black screen. In case the plane of the screen was not exactly parallel with the vertical plane passing through the eyes of the larva, the reaction was not represented by the simple forward rotation, but was modified by side movements.

Case 21—When the larva was in the normal swimming position and the black screen approached from the side, several reactions might occur. Most commonly the larva underwent a swing of its longitudinal axis so that the head was brought to face the screen. Another reaction sometimes observed was a rolling, or revolution, on the long body-axis, in such a manner that the back moved away from the screen. At the same time there occurred a swing of the longitudinal axis which caused the head to be directed toward the screen. These two reactions might occur simultaneously, and the resulting reaction be a blending of the two components mentioned above. The rolling on the longitudinal body-axis was seldom over 90° from normal (back above), usually less. Yet in cases where the illumination in the dark box was greater, or when the screen was introduced suddenly, the rolling motion might exceed 90° , and the larva fall to the bottom of the container.

Case 22—In this instance the larva oriented in the normal swimming position and the screen was made to approach from above. This combination produced several forms of reaction. In cases where the general illumination in the container was not great, the larva merely experienced a slight change in the direction of the longitudinal body-axis; the head assumed a superior position, so that the long axis of the body was nearly horizontal, or even directed upward at a small angle, rather than bent downward at an angle of 30° from horizontal, as in the normal swimming position. On the other hand, if the illumination was greater, the larva might undergo a rotation on its own longitudinal axis through 180° and fall, back downward, to the bottom. Whatever reaction occurred, it could be explained as an effort of the larva to turn the head toward the black screen, and the degree to which this was attained depended very much upon the intensity of illumination throughout the container. The type of reaction mentioned above was demonstrated to better advantage

in the following experiment. A large tube containing a number of larvæ was placed in an upright position on the laboratory table, and the upper half covered with a roll of black paper. The larvæ gathered in the more brightly illumined end of the tube, which was below. So long as they swam in the lower part of the illuminated area, they assumed the normal swimming position, but whenever they came into the upper regions, and approached the edge of the black paper, the direction of the longitudinal body-axis was changed from 30° below horizontal to 30° or even more above the horizontal plane.

Case 23—In the following case the larva was oriented in the normal swimming position and the screen was made to approach from below. As a result the larva usually reacted by a slight forward rotation, the head passing through an arc of a few degrees, and producing a still greater angle between the longitudinal axis and the horizontal plane. This new swimming position was seldom subject to further modifications so long as the light conditions remained unchanged. Regarding the reactions of the larvæ of *Homarus vulgaris* under similar experimental conditions, BOHN (1905, p. 11) remarks: "Si la larve nage le dos dirigé le haut, il y a roulement de 90° ou de 180° , la par suite la larve dévie lateralement ou tombe."

Such a result as the above was not observed by the writer. On the other hand, it was observed that, whatever the body-orientation of a group of larvæ might be previous to the approach of the black screen from below, its presence usually determined a rise of the larvæ from the bottom of the container to the upper waters, where normal swimming was manifested so long as the screen beneath remained in place. When it was removed, however, or replaced by a white screen, the consequent reaction was, as we have already seen, characterized by rotations and revolutions through 90° or 180° . These reactions in turn resulted in bringing the larvæ again toward the bottom, and in determining a consequent absence of larvæ in the regions near the surface of the water.

Case 24—In this instance the larvæ were oriented with back below, and the black screen was made to approach from behind in such a manner that the plane of the screen was parallel with a vertical plane passing through both eyes of the larva. Under these conditions (see Fig. 14, *A'*) the reactions were as follows. When the black screen, *G.* was introduced, the larva, *A'*, under-

went a forward rotation through an arc of 180° , and assumed the normal swimming position, B' , with the back uppermost and the head facing the screen. This orientation was maintained with a greater or less degree of constancy so long as the conditions of light remained the same. If, on the other hand, the screen was so placed, or the larva had such a position, that the plane of the screen was not exactly parallel to the vertical plane passing through the two eyes of the larva, a different reaction was experienced. In this instance the first response was a revolution on the longitudinal axis, usually through 180° . This resulted in bringing the back of the larva uppermost, and was usually followed by a swinging of the longitudinal axis, which brought the head to face the screen. The direction of this side swing (to the left or the right) was determined by the angle which the longitudinal axis of the larva made with the screen. For instance in Fig. 15, the larva designated A' would swing to the right, while the larva designated C' would swing to the left, each in the direction indicated by the arrows. In other words we may say that the larva would swing in that direction which brought the head, by the shortest course, to face the screen. But the two reactions mentioned above might, as in previous cases, be blended to form a composite reaction, which differed from either of its simple components.

Case 25—In the present instance the larva was oriented lying on its back and the screen was introduced from before. Under these conditions, as in Case 19, there was no modification in the body-position. In certain instances the larva underwent a revolution through 180° on its longitudinal axis and assumed a position with back above and head still directed toward the black screen; but in the great number of cases the orientation remained unchanged.

Case 26—In case the larva was oriented with the back below and the screen was made to approach from the side the reactions were as follows. The larva experienced a rolling or revolution on its longitudinal axis, in consequence of which the back moved away from the screen through an angle of 90° , occasionally more. At the same time there was a swinging of the longitudinal axis, itself, so that the larva came face to face with the screen, eventually with the back uppermost. During this reaction the larva often departed from the screen. As in Case 21, mentioned

above, these two reactions might occur at the same time, and then the resulting reaction was a composite.

Case 27—In the present case the larva was oriented with back below and the black screen was introduced from above. Under these conditions it usually underwent a slight forward rotation with a consequent rise from the bottom, and came into a new swimming position with the longitudinal axis directed somewhat upward as shown in Fig. 20, *B'*.

Case 28—In this instance the larva was oriented with back below and the black screen was introduced from beneath. The reactions were usually as follows. The larvæ underwent a revolution of about 180° on its longitudinal axis, and assumed practically the normal swimming position, with the back uppermost and the head bent downward at an angle of about 30° . In other cases, however, this new position was brought about by a different sort of reaction; namely, a backward rotation through an arc of 180° . This resulted in throwing the larva again into the normal swimming position.

Generally speaking, we may say that, when black or white screens were made to approach larvæ of any one of the first three stages, diversely oriented, the larvæ manifested two forms of response. First, a motor reflex, which tended to place the longitudinal axis in a certain relation to the plane of the screen; secondly, and subsequent to the first response, a progressive orientation, toward or away from the screen, as the luminosity of the screen, the physiological state of the larvæ, and other conditions of the case, determined. When the white screen was used, the larvæ commonly became oriented with the head directed away from the screen. In the case of black screens, on the contrary, the head was directed toward the screen and the back more or less away. These reactions occurred whether the screens were made to approach from above, below, behind, or the side. After body-orientation had taken place, the larvæ might approach or recede from the black or the white screen, according as they were reacting positively or negatively.

The mechanics of reaction upon which orientation to the screens was found to depend, agree, for the greater part, with the types of reaction to black screens reported by BOHN (1905), who has made a careful study of the effects of causing a black screen to approach the larvæ of *Homarus vulgaris*, diversely oriented. There are,

however, certain disagreements. First, it is certainly true that bringing the black screen parallel to the longitudinal axis of the larva frequently determined a rolling of the larva on its own longitudinal axis, whatever the original orientation may have been. But in Case 21, certain orientations of the larva were noted in which these rollings did not occur. It is true, moreover, that the progressive orientation often took place in that direction in which the back was directed. But several instances were observed wherein the orientation to the black screen resulted merely from a swinging of the longitudinal axis of the larvæ so that the head was directed toward the screen and where consequent progressive orientation was either a movement backward or forward, head foremost or tail foremost, as in positive or negative phototaxis.

We have now examined somewhat in detail the effects of sudden illumination and of sudden shading, the effects of white screens and of black. If we now compare the detailed results of these studies, we note that the effects produced by introducing a white screen are comparable with those obtained by suddenly admitting illumination, while the results brought about by black screens are comparable to those determined by suddenly cutting off the light. In other words, the larvæ appear to respond to the influence of screens of black and white by reactions which are dependent upon the same simple forms of response observed under the conditions of direct lighting and shading.

In view of this correspondence in the nature of reaction to direct lighting and to screens of black and white, it may be considered probable that the screens and backgrounds are instrumental in determining the behavior of the larvæ, only in so far as they are themselves the source of (reflected) illumination. Thus, when the black background causes a swing of the larva, as a result of which it comes to face the screen, we cannot say that the primary factor is the blackness of the screen; but rather that the small amount of light reflected from the screen permits rays of light from other directions to become effective. The larva "heads" to the black screen because his eyes encounter no light rays coming from this direction; and he turns away from the white screen because his eyes encounter stronger reflected light from this than from any other direction.

The effect of backgrounds—The question of the influence of backgrounds in determining the orientation of crustacean larvæ

has been brought forward by KEEBLE and GAMBLE (1904). Aside from the effects of screening, the more general problem of backgrounds did not receive especial attention in the course of the present investigation, but, as we shall see, the question of screening which we have discussed in the preceding section is probably only a single phase of the problem of backgrounds. The following experiments which were performed more or less at random in connection with other experiments, but which deal with the question of backgrounds, may, however, be presented.

By the term background, as it is used in the present case, is meant the permanent color-tone of the surrounding walls (as a whole or in part) which confined the young larvæ. This condition was somewhat different from that determined by the use of screens which were movable and could be placed at any angle with reference to the body-axis of the larvæ. Backgrounds were employed in several different ways. They were sometimes represented by the black or white lining of the reaction boxes; again, by the ground upon which the glass dishes or tubes rested, and in still other cases by the outer covering of these dishes, or tubes. The subject may be considered under two heads: (1) the effect of backgrounds in connection with the purely photopathic response; (2) their effect in determining the "choice" of a particular region of light-intensity when phototaxis also is operative. In view of the fact that the investigation of the first phase of this problem was not undertaken in the present work, we may pass directly to the consideration of the second point stated above.

The effects of backgrounds in connection with both the phototactic and the photopathic response—Under this head we may consider those conditions of experiment, which, although they be chiefly productive of reactions to the directive influence of the light, nevertheless were modified by response to the intensity of the light. These conditions were secured by the use of Y-tubes. The following experiments serve to show why, in the case of the larval lobsters, the tendency to gather in the brighter areas (assumed positive photopathy) is often associated with positive phototaxis; and why a tendency to gather in the darker areas (assumed negative photopathy) may be associated with negative phototaxis. In the diagrams of Fig. 21 are represented the Y-tubes as set up for experiment. Those whose arms are above were arranged for experiment with larvæ having positive phototactic reaction; those

whose arms are at the bottom, for larvæ having a negative phototactic reaction. In tubes *A* and *B* one side of one arm was fitted with a band of black paper which extended half over the circumference of the arm and a very short distance down each stem. In tubes *C* and *D* the same arrangement existed, save that white instead of black paper was used. In every case the light rays came from the window in the direction of the arrows. In all cases of larvæ manifesting a negative reaction, the start was made at the end of the tube (lying horizontally on the table) nearer the window. In the case of positively reacting larvæ, the start was made from the end of the tube farthest from the window. The end marked *a* in every instance was the end *from which* the larvæ moved, the purpose of the test being to determine in which arm of the tube the larvæ would eventually gather.

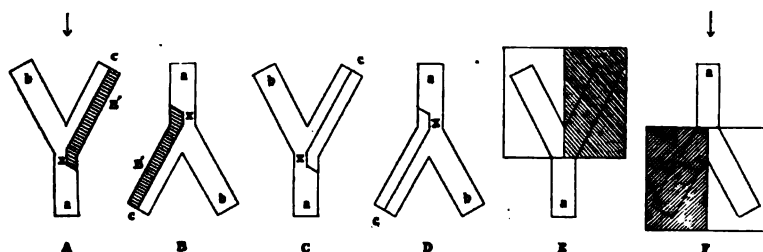


FIG. 21. Showing the Y-tubes set up for experiment. In every case the light came from above in the direction of the arrows. The tubes whose arms are above were set up for positively reacting lobsters; those whose stems are above, for negatively reacting lobsters. In tubes *A* and *B* the cross-hatched areas represent the part covered with black paper. In tubes *C* and *D* the clear area was covered with white paper. Tubes *E* and *F* are shown equipped with the glass plates placed over the arm. In every instance the larvæ were started from the end of the tube designated *a*. For further explanation, see *Cases 29-33 inc.*, pp. 286-289.

Case 29—The tube was arranged as in Fig. 21, *A*. Ten positively-reacting, first-stage larvæ were placed in the Y-tube, and, by certain manipulations of the light and by virtue of their positive reaction, they were made to congregate in the stem end. Then suddenly, the direction of the light was changed so as to come in the direction of the arrows. Immediately the larvæ oriented with their heads toward the end *a*, and passed through the tube toward the light. As soon as they approached the region marked *x* they came under the influence of the dark background bounding the side of the tube. Immediately, as we have seen to be the case in previous instances, the longitudinal body-axis swung so that the

head came to face, more or less obliquely, the dark background, *B'*. The directive influence of the rays, however, continued to draw the larvæ on, but since they must travel in the direction in which the tail pointed, they entered the arm *b*, and passing close to the inside continued until further progress was prevented by the end of the arm. Space will not be taken to show the numerical results of this and similar experiments. Suffice it to state that nearly all of the positively reacting larvæ, of whatever stage or age, when submitted to these conditions of experiment, reacted as has been described above. This experiment was modified by placing the Y-tube so that the uncovered arm of the tube rested upon a piece of black paper. The results were invariably the same; the majority of the larvæ progressed to the arm of the tube not overlying the black ground.

Case 30—In this case the conditions of the experiments were further modified by reversing the Y-tube so that the arms pointed away from the window. In this instance larvæ which were manifesting a negative reaction were employed, and were first placed in the end (*a*), nearer the window. When the light was admitted the larvæ at once oriented with their heads directed away from the light and began to move away from the window. When they had reached the point designated *x*, they immediately underwent a swing of the longitudinal axis, as in previous cases, so that the head was directed toward the black ground, bounding the outer surface of the arm *c*. Thus they would continue, passing close to the inner wall of the tube until the majority had gathered in this arm. In this instance, however, the larvæ would usually rest between *x* and *c*, instead of moving to the end of the arm.

Case 31—Here the black background bounding the outer side of one arm was exchanged for a white ground of the same size and having the position shown in Fig. 21 *C*. Third-stage larvæ giving a positive reaction were employed for the experiment. They were started in the end *a*. When the light was admitted, the usual body-orientation resulted, and the larvæ began their progression through the tube toward the window. When they had arrived at *x* they came under the influence of the white ground and turned their heads away from this side. Progressive orientation then continued and the larvæ eventually became grouped in arm *c*. Similar results were obtained when half of this arm of the tube was laid over a sheet of white paper.

Case 32—The previous experiment was further modified by reversing the Y-tube so that the arms were directed away from the window (Fig. 21, *D*). Larvæ which were giving a negative reaction were employed. They were placed in the end *a*, and the light was admitted. After the usual body-orientation had taken place, the progression away from the window began. When the larvæ reached the point *x*, and had come under the influence of the white ground bounding one side of the tube they would swing their heads toward the right and continue their progress until all were gathered in arm *c*. This was somewhat unexpected. It eventually transpired, however, that the white ground bordering the outer surface of the tube did not act as a reflector or intensifier of the light rays, but as an opaque shield, cutting off the rays which would otherwise have entered the arm *c*. Thus, as in Case 30, the negatively reacting larvæ had merely grouped themselves in the arm where the light was least bright. When the Y-tube was so placed that half of arm *c* rested upon a sheet of white paper the result was different. The larvæ congregated in arm *b*, which was, under these conditions, the region of least light intensity.

Case 33—The four cases mentioned above were supplemented by other experiments involving the use of colored glass plates. As described in Experiment 15, these plates were so placed over the arms of the Y-tube that a difference in the intensity of light striking one arm was caused by interposing a red, orange or yellow glass plate between that arm and the source of illumination. In these cases the positively reacting larvæ gathered in the arm where the light-intensity was the greater, while the negatively reacting larvæ grouped themselves in the arm where the light was least bright. As a rule, the larvæ of earlier stages seemed to be more susceptible than the others to slight differences in the intensity of light at the entrance to the arms.

Thus is explained the tendency for positively reacting larvæ to gather in regions of greater light-intensity, and on the other hand, the tendency of negatively reacting larvæ to congregate in regions of lesser light-intensity. This condition of affairs has, no doubt, given many investigators reason to believe that such reactions are but manifestations of a positive photopathy; and that photopathy and phototaxis are fundamentally the same. We now know, however, that the reaction just described in Case 5 is due to the combined effects of two tendencies; the one to turn the head

toward the dark areas (areas of non-stimulation); the other to move in the direction of the longitudinal axis of the body either toward or from the source of light. Were we dependent upon such experiments as these for our belief in the existence of a separate response to light-intensity, regardless of directive influence of light, we might well say that the photopathic and phototactic responses are, in the end, one and the same. But the writer has adduced in the previous section other data which separate more clearly these two types of reaction.

VII. ANALYSIS.

It has for some time been the custom to state that certain organisms are positively phototactic or positively photopathic, and that other organisms are negatively so. The index of reaction for several crustaceans has been so recorded, but the observations are usually incomplete, often uncritical, and sometimes of questionable significance. It is true that, in a very general way, organisms react positively or negatively to light. For instance, it may be said that the lobster shuns the light, that *Palemonetes* is attracted by the light, and that the larvæ of *Limulus* avoid the light. The definite statement, however, that the larvæ of *Limulus* are negatively heliotropic, or that *Palemonetes* and larvæ of *Homarus* are positively phototactic, is as inadequate as would be a biography written on the basis of a single day's association with a human individual. It may be true that by the time the adult stage is reached, the reactions of many animals have become more or less stereotyped, so that reactions like those of the moth to the flame, are easily predictable. In the larval and adolescent stages, on the other hand, the reactions are frequently more variable. To say that the lobster of the second larval stage is positively phototactic or positively photopathic is, as has been demonstrated, by no means a correct interpretation of the facts of the case, for slight changes in the conditions of stimulation may be sufficient to reverse the index of reaction. This variability doubtless occurs in many arthropods. It thus becomes evident that, although the young lobsters may be regarded as machines upon which many different external forces act and cause certain reactions, still (except for the definite body-orientations which are invariably determined by the directive influence of the light rays) they are

machines the nature of whose operations can seldom be predicted unless the age, the stage, the kind and degree of the stimulus, are accurately known. These conditions of reaction indicate the extent to which the behavior of young lobsters is determined by their physiological states; and the foregoing experiments show in what way these physiological states change, not only from one stage-period to another, but even during the same stage-period, through the influences of metabolism, development, and perhaps still other factors. The extent to which the natural behavior of animals in their natural environment can be explained on the basis of the results of laboratory experiments depends largely upon the animal and the kind of reactions involved. It is quite probable that some of the characteristics of reaction, which have been described in the present paper, determine in a large measure, the daily behavior of the larval and early adolescent lobsters when they are in their natural environment. Unfortunately, however, we know too little regarding the behavior of lobsters under natural conditions, to attach great importance to far-reaching explanations of their daily activities on the basis of laboratory experiments. A few points, however, may be noted. The reports of biological surveys make it clear that, at the surface of the ocean or of bays in which lobsters are known to live and breed, the stage most often taken in the tow-nets is the fourth; the larval stages are much less frequently found, the fifth stage seldom, and later stages never. Observations which were made on lobsters of different stages taken from the Wickford hatchery and liberated in the surrounding waters of Narragansett Bay yield similar evidence regarding the immediate natural distribution. In these cases the lobsters of the larval stages were found to swim for a brief time, then gradually disappear from the surface; the fourth stage lobsters swam actively at the surface so long as they were observed; while the fifth and all later stages plunged at once into the deeper water and were immediately lost to sight.

As the writer has already suggested, it is impracticable to attempt to explain the natural behavior of larvæ of the first three stages, on the basis of the reactions which have been discussed at some length in the present paper. The light (depending upon its intensity and directive influence; and upon the age, stage, and previous condition of the larvæ) may determine at one time a positive, at another a negative, response, so that the general reaction

of groups of lobster larvæ can in no way be readily predicted. One exception to this may be stated. The first-stage larvæ, directly after hatching, would be strongly drawn to the surface of the water by virtue of both their photopathic and of their phototactic response. After the first day or two, however, begins that modification and variation in the phototactic action which, for groups of uncertain age and condition, makes any accurate prediction of their movements quite impossible.

In the case of the fourth-stage lobsters there is a better basis for the correlation of the natural and experimental types of behavior. We know that, under experimental conditions, hungry fourth-stage larvæ, when submitted to food stimuli, will rise immediately to the surface of the water and swim about excitedly for some moments; we know also that the early fourth-stage larvæ, under certain experimental conditions will leave a region of low light intensity and remain in regions of greater light intensity. We have learned, moreover, that the same fourth-stage larvæ, under different experimental conditions, will usually shun the light when it has a single directive influence, and travel in the direction of the rays away from their source. Finally, we have observed that the fourth-stage lobsters, except in the latter part of the stage-period, show a definite tendency to remain at the surface of the water.

The question now arises: What is the cause of this surface-swimming? Is it a response to the intensity of light, to the directive influence of light, to hunger, or to gravity? Although we know something of the effects of several of these factors when they act separately, it is difficult to ascertain their individual influence when they work in combination. If, however, we can discover any parallel between a certain type of reaction under experimental conditions and a certain mode of behavior under natural conditions, and find that as one is modified or lost the other is also, then, and then only, are we justified in believing that we know the determining cause of the particular type of natural behavior in question. We have such a parallel between the photopathic (and occasionally the phototactic) reactions and the surface-swimming tendency of the fourth-stage lobsters. As the former becomes modified and is eventually replaced by the negative reaction, so the latter is changed and finally gives way to the bottom-seeking tendency as the lobsters pass on through the fourth stage-period. With

such a parallel before us, it cannot be doubted that there exists a certain causal relation between the positive photopathic reaction and the surface-swimming tendency on the one hand, and the negative photopathic reaction and the bottom-seeking tendency on the other. But the photopathic reaction may not alone be responsible for the surface-swimming tendency on the part of the fourth-stage lobsters. The presence of food particles in the water excites them strongly, and causes them, when in the glass jars, to swim excitedly at the surface of the water. It therefore appears quite within the bounds of possibility that chemotropism may also play a part in determining the surface-swimming of the fourth-stage lobsters.

The explanation of the behavior of the fifth and all later stages, in the light of the foregoing experiments, rests upon a more certain basis. We have observed that the fifth-stage lobsters invariably manifest both a negative phototactic and a negative photopathic reaction. In general this may be said to explain the fact that lobsters in the fifth and all later stages shun the light at all times. Little work was done on the behavior of the older lobsters, and it is hoped that future investigations may continue along this line.

In connection with the mechanics of orientation, the writer has shown that the reaction of larval lobsters to light is made up of two components—body-orientation and progressive orientation; and that the former is primary while the latter is secondary. In the earlier pages of this paper it was demonstrated that the *progressive orientation* is dependent upon a great number of conditions, and that the orientation responses are relatively complex reactions which are dependent in great measure upon the obscure, changing, internal conditions which are embraced under the general term, "physiological states." In later pages, on the other hand, attention has been directed to those conditions of light which determine the *body-orientation* alone; and the results recorded have made it clear that the movements producing the body-orientations are types of action which simulate more closely pure reflexes, direct, constant, and invariable.

As BOHN (1905a) has well said, it is impossible to take definite account of the complicated series of phenomena which take place in the nervous system of animals even as low as the arthropods, for these are dependent not alone upon complicated connections between neurons, but also upon their variable states. Yet it is

apparent that this difficulty applies rather (at least in the reactions of the larval lobsters) to those movements which determine the *progressive orientation* to light, than to those which determine *body-orientation*. Even in the latter somewhat less complicated and more easily explained phenomena, however, we are still far from recognizing the underlying causes.

It is true that we can understand in a way why the "posterior position" of the thoracic appendages determines a negative response, while the "anterior position" determines a positive response. We can, moreover, understand why a more intense illumination of the eye on one side causes a greater activity of the swimmerets on that side, and a consequent swing of the larva away from that side. This phenomenon was well shown by experi-

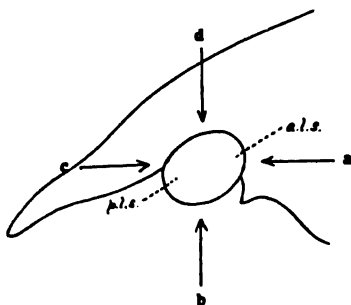


FIG. 22. Diagram showing the rostrum and one eye of a larval lobster; *a, b, c, d* represent direction of light striking the eye from behind, below, in front and above; *a.l.s.* represents posterior lateral surface; *p.l.s.* represents anterior lateral surface. For further explanation, see p. 297.

ments which the writer performed upon larvæ with blinded eyes (HADLEY 1908). These experiments demonstrated that, when the right eye was blinded, the direction of forward swimming was invariably to the right; in other words, the exopodites beat more vigorously upon that side of the body whose eye was most stimulated, and the larva was, in consequence, "pulled around" like a boat. These reactions are explainable on the grounds of a heterolateral stimulation and a consequent unequal action of the muscles on the two sides of the body. But we do not understand as clearly how or why the action of the light striking with equal intensity the corresponding areas of the posterior surface of the eyes (Fig. 22), for instance, brings about these "anterior" or "posterior" positions of the thoracic appendages, and the con-

sequent positive or negative reactions. Nor do we understand why, when the larva is in one "physiological state," a certain intensity of light (striking equally the posterior lateral surface of the two eyes) causes a positive reaction, while if the same larva is in another "physiological state," the same light (striking with the same intensity the same parts of the eye-surfaces) causes the opposite reaction; or again, why when the larva is in the *same* "physiological state," one intensity of light causes a positive reaction, while light of slightly less intensity determines a negative reaction. No more do we know why the illumination of the upper surface of the eyes (Fig. 22, *d*) causes a forward rotation; or the illumination of the lower surfaces (*b*), a backward rotation; or the illumination of the anterior surface (*c*), a forward or a backward rotation. These as yet unexplainable conditions of reaction may well convince us that, however simple and mechanical some of these reactions appear to be, many of them are extremely complex, and indicate a very complex relation between the different regions of the eyes and the nervous centers. Yet, as has been stated, to such a degree as any of these reactions can be explained, those which are concerned in the processes of body-orientation are more easily interpretable on the "simple-reflex" hypothesis. In view of this fact the writer would differ from the conclusion reached by BOHN (loc. cit., p. 41): "Tous ces phénomènes (the reactions of larvæ of *Homarus vulgaris*) sont en relation avec des états physiologiques particuliers. Sous l'influence de l'éclairement, l'état physiologique des larves de homard ne tarde pas à changer, et les tropismes aussi." The present writer would limit the application of this theory to those reactions of the larval lobsters which are concerned with progressive orientation, excluding body-orientation.

Regarding the relation of the type of reaction found in the larval lobsters to the tropism theories, inference has already been made in the preceding paragraphs. First, to what extent does the behavior found in the larval lobsters agree with the local action theory of tropism? The primary demand of this theory is that the body of the organism should become so oriented with respect to the source of illumination that the anterior end is made to point either toward or from the source. Under these conditions the index of reaction is said to be positive or negative, according as the organism moves toward or from the light. "This

orientation is produced, according to this tropism theory, by the direct action of the stimulating agent on the motor organs of that side of the body on which it impinges. A stimulus striking one side of the body causes the motor organs of that side to contract or extend or to move more or less strongly. This, of course, turns the body till the stimulus affects both sides equally; then there is no occasion for further turning and the animal is oriented" (JENNINGS 1906a, p. 266). This is also brought out by HOLT and LEE (1901, p. 479), "The light operates, naturally, on the part of the animal which it reaches." Thus, this tropism theory requires that, in order to determine the direction of movement, the stimulus must act more strongly on one side of the body than on the other. It is needless to say also that in the majority of cases the same conditions of stimulus which cause an animal to direct the head away from the source of the stimulus, also determine a movement in the same direction. Therefore, if we separate, as has been done in this paper, *body-orientation* from *progressive orientation*, we can say that, in most organisms, the index of body-orientation agrees with that of progressive orientation; the conditions of stimulation which cause the one likewise determine the other. Let us now see to what extent the behavior of the larval lobsters agrees with these requirements of the local action theory of the tropisms. In order to treat the matter concretely we must consider it under two heads. First, body-orientation; then, progressive orientation.*

It has been shown in the previous pages that, whatever the sign of progressive orientation may be, the *body-orientation is invariably negative*; and that this body-position is produced as a result of diverse reactions which are attributable to the relative intensities of light which strikes the eyes of the larvæ. This body-orientation, moreover, is constant; it is not dependent upon the age, stage, previous stimulation, hunger, "physiological state," or upon any modifications of the external stimulus, such as changes in intensity, duration of stimulation, etc. The orienting reaction always comes about in the same way, so that we here have a case where the "same-stimulus-same-reaction" principle invariably holds. In other words, the reactions by which the larval lobsters secure the characteristic body-orientation are typical and invariable motor-reflexes.

Beyond producing the body-orientation, the direct motor-reflex

ceases to influence the behavior of the larval lobsters. From this moment on, a multitude of conditions appear to be brought to bear to determine the consequent *progressive orientation* of the young animals in one sense or the other. No longer can we say, "same stimulus, same reaction" (SPAULDING 1904), for there is now no constant form of reaction even to the same stimulus. The reactions appear to be no longer so dependent upon the nature of the *external* stimulus, but are more largely regulated by the "physiological states." This we might consider as the cumulative result of a long series of previously acting stimuli, to which others are constantly being added with two effects; first, of bringing about a definite reaction determined by the nature of the stimulus and by the present physiological state; second, of further modifying the physiological state itself, so that even the reapplication of the same stimulus might provoke a quite different reaction. It can not be doubted that the series of changes, which occur in the behavior of the lobster larvæ as they pass through the successive stages, is largely due to this gradual modification of the physiological condition—the cumulative effect of a long series of antecedent stimuli.

We may sum up the preceding paragraphs by saying; (1) The reactions by which the *body-orientation* of larval lobsters is produced are invariable motor reflexes, and the method of such orientation is, therefore, quite in accord with the requirements of the local action theory of tropisms. (2) The reactions by which the *progressive orientation* is produced, although appearing to be simple reflexes, are not invariable but are dependent upon many conditions of stimulation, and especially upon the physiological states.

In view of these facts, it appears that, while the body-orientation of the larval lobsters is not of primary importance in determining the index of the progressive response to the directive influence of the light rays (since the body-orientation and the progressive orientation are dependent upon quite different factors), still it is of primary importance in determining the general line along which the movement shall take place, either toward or from the source of light. It is shown by these points that this type of response is not in agreement with JENNING's theory (1906b), in which the process of orientation is of secondary importance, for neither the immediate nor the final body-orientation of lobster larvæ to light

can be characterized as a "selection from among the conditions produced by varied movements" (JENNINGS 1906b, p. 452). Indeed there are no "varied movements" in the reactions by which the body-orientation to light is brought about. The only way in which the term "random movements" can be applied to the orientation of the larval lobsters is in its relation to the variable extent of the revolutions or rotations. It cannot be denied that this *degree* may be dependent upon the physiological states of the larvæ (for instance, fatigue or freshness), but, after all, this point is irrelevant to the present discussion, since it is the direction of the immediate turning and not the extent of it, which is the important consideration.

The foregoing experiments throw but little light upon the question of intensity of light versus direction of light. Indeed it is probable that the latter phase of the problem is not of great importance except in cases where the light rays are effective by passing through the body as in the case of the electric current, which, as the writer has shown elsewhere (HADLEY 1907a) causes reaction only when the direction of the current holds a certain relation to the longitudinal axis of the larvæ. It is clear, however, that the direction of the light rays does modify the reactions of the larval in two ways: (1) By determining *which of the two eyes shall be most stimulated*, thus causing a body-orientation in which the longitudinal body-axis is thrown into line with the direction of the light rays, so that the eyes shall be equally stimulated; (2) by determining *what parts of the surfaces of the two eyes shall be stimulated equally*, and thus producing a body-orientation in which the posterior lateral surface (Fig. 22, *a.l.s.*) of the eyes receives the strongest stimulation, and the anterior lateral surface (*p.l.s.*) the least. These reactions, and the consequent progressive orientations of the larvæ, the writer has called reactions to the directive influence of the light. That there may be, in addition to these responses, reactions to the intensity of light as HOLMES (1901) and others have considered possible, it is still permissible to believe, and in the earlier pages of this paper the writer has pointed out some reactions of larval lobsters, which, although not perfectly understood, may be included under the head of photopathic response.

The foregoing experiments were carried on at the Experiment Station of the Rhode Island Commission of Inland Fisheries at

Wickford, Rhode Island, where exceptional facilities were found for obtaining material of all ages and stages. The writer's thanks are especially due to Prof. A. D. MEAD of Brown University for making possible an opportunity for this line of inquiry and for material assistance; to Dr. R. M. YERKES of Harvard University, and to Dr. H. E. WALTER of Brown University for friendly criticism during the preparation of the paper; also to Mr. E. W. BARNES, Superintendent of the Wickford hatchery, for many kindnesses.

VIII. SUMMARY.

1. Larval and early adolescent lobsters present both phototactic and photopathic reactions as these responses are defined on p. 201.

2. There is no constant type of response for all larval lobsters, but a modification of reaction occurs through the metamorphosis of the larvæ.

a. First-stage larvæ, directly after hatching, give definitely positive phototactic and photopathic reactions which endure for about two days, after which the phototactic reactions change to negative, becoming positive again shortly before moulting into the second stage.

b. Both early second-stage and early third-stage larvæ manifest a negative phototactic reaction, which usually becomes positive shortly before moulting into the third and fourth stages, respectively.

c. The photopathic reaction of the first three larval stages is commonly positive from the beginning to the end of the stage.

d. The phototactic reaction of the fourth-stage lobsters is usually (i. e., except in cases where intense light is used in connection with early fourth-stage lobsters) negative throughout the stage-period, and the photopathic reaction, positive during the early fourth stage-period, eventually becomes negative.

e. During the fifth stage-period, and in all later stages, both the phototactic and the photopathic reactions are strongly negative.

3. While the photopathic reaction of the larval lobsters remains constant, the phototactic reactions are subject to modification as a result of changes in the intensity or in the direction of light.

a. During the early first stage-period no intensity of light used changes the index of the phototactic or of the photopathic response, but later an intense light may reverse the index of the phototactic reaction.

b. Throughout the second and third stage-periods, the index of the photopathic reaction is not reversible, but during the early part of these periods the negative phototactic reaction, and during the latter part the positive phototactic response, may be reversed temporarily by using light of great intensity (suddenly introduced).

c. During the fourth stage-period the negative phototactic response can not be reversed (except in such instances as are noted in Exp. 24, Cases 5 and 6), but the positive photopathic reaction of the early fourth stage-period may be reversed temporarily by using light of very great intensity.

d. None of the negative responses of the fifth-stage lobsters can be reversed by using light of any intensity whatsoever.

e. Submitting larvæ to darkness for periods of 2 to 12 hours does not change the index of reaction.

4. The reactions to light can be modified by other factors; contact-irritability is first manifested in the middle or later part of the fourth stage-period, and henceforth determines (about equally with light) the behavior of early adolescent lobsters.

5. Laboratory experiments explain some of the aspects of the behavior of the young lobsters under natural conditions of environment: (1) The positive photopathic reaction, and the positive phototactic reaction (to lights of very great intensity) together with the response to food stimuli may unite in determining the surface-swimming of the early fourth-stage lobsters. (2) The negative photopathic reaction, the negative phototactic reaction together with the response to contact-stimuli may unite in causing the late fourth, fifth and all later-stage lobsters to leave the surface water, and to burrow at the bottom of the sea.

6. The reaction of larval lobsters to light depends upon two factors; body-orientation and progressive orientation.

7. The body-orientation is invariably negative and is due to the difference in illumination of the two eyes of the larva. It is brought about by invariable reflex movements which tend to bring the longitudinal axis of the body parallel to the rays of light, with the head away from their source.

8. The progressive orientation may be either positive or nega-

tive, and is due to the position (extension or contraction) of the thoracic appendages. If these have the "anterior position," the reaction is positive; if they have the "posterior position," the reaction is negative. These positions appear to depend upon the intensity of light which strikes the posterior lateral surface of the eyes equally.

9. The larvæ orient to screens and backgrounds of black and of white by reflex movements identical with those by which they react to direct illumination and shading.

10. The reactions by which the body-orientation to light is produced, are invariable motor-reflexes, quite in accord with the local action theory of tropisms. The reactions by which the progressive orientation to light is produced, although appearing to be simple reflexes, are not invariable or constant, but dependent upon "physiological states."

11. In all the reactions to light (except the photopathic) the body-orientation is of primary importance, since progressive orientation cannot occur until the body-orientation has been established.

12. None of the reactions to light can be interpreted as "a selection from among the conditions produced by varied movements." They are not trial (and error) reactions, in the sense in which this expression is used by JENNINGS and HOLMES.

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THE REACTION TO LIGHT OF THE DECAPITATED YOUNG NECTURUS.

BY

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During the summer of 1904 a large number of young Necturi (15-18 mm.) were decapitated by pinching with fine forceps. The heads were cut off, at slightly different levels, at about the exit of the common trunk of the seventh and eighth nerves. Although the percentage of fatalities ran high, many of the larvæ lived until the yolk was absorbed, usually about three months. The larvæ used in the following experiments were decapitated on July 10 and in early September they had grown to a length of 30 mm.

That the young and old Necturi are negatively phototropic is a matter of everyday observation both in the natural environment and in the aquarium.

In testing the effects of various kinds of light on the normal and decapitated larvæ they were placed in a small glass aquarium about 60 cm. long, 30 cm. deep and 25 cm. wide. One-half of this aquarium was then painted black and the top covered with a black board. The larvæ, both normal and decapitated, were then subjected to sunlight of varying degrees of intensity. The rays were condensed by a hand glass and by concave mirrors, and were also passed through ground glass. The light of the room was controlled by an opaque curtain so that varying degrees of intensity could be obtained.

In order to test the effects of artificial light, the normal and decapitated larvæ were taken into a photographic dark-room and the aquarium was placed in such a position that a sixteen candle-power electric light illuminated one-half of the aquarium. In the same manner one-half of the aquarium was exposed to the light from an arc lamp. Further experiments were made by controlling these lights with condensers and mirrors. In all cases both the

normal and the decapitated animals, when together or separate, react in the same manner as they do in diffuse daylight and direct sunlight. They are negatively phototropic.

In case the normal larvæ are unable to escape a bright light they almost invariably orient themselves in such a position that the light falls with equal intensity upon the two sides of the body. It was also noted that in the great majority of cases the heads were turned toward the light. The decapitated individuals showed the same orientation, except that the heads were about as frequently turned from the light as toward it.

A sharp pencil of rays of either sunlight or electric light when thrown on the tail of the normal animal causes a quick response. This indicates that the tail is especially sensitive, which is in agreement with the observations of DUBOIS on *Proteus*. In the same manner the decapitated animals respond more readily when the rays are concentrated upon the tail than when they are concentrated on other parts of the body.

During the summer of 1902 larvæ were reared in glass aquaria, beneath which were placed pieces of black, white, red, yellow, green and blue paper. Although a large number of counts were made to determine the percentage over the different colors, at successive intervals, there seemed to be no decided preference for one color over another. A second set of observations, the following year, seemed to show that by far the highest percentage of larvæ were found over the green, whether this was placed on the side of greatest or least diffuse daylight.

In 1905 the same experiment was repeated with the decapitated larvæ, but fifty-two counts showed nothing definite beyond the fact that the larvæ were most frequently found on the colors in the half of the spectrum toward the violet end.

It is of interest here to recall that DUBOIS ('90, p. 356) says: "I have observed that *Proteus*, under the same condition as the blinded Triton, shows a preference for the following colors in a decreasing series: first, dark, then red, yellow, green, violet, blue and white light." In the *Proteus* with normal eyes DUBOIS found the reaction towards the various colors was in the following decreasing series: first, dark, then yellow, then green, red, blue, violet. It should be added that these results were not obtained with monochromatic light.

Concerning the reactions of Amphibia to light, there is some

difference of opinion. The earlier observations of GRABER ('84, p. 121) seemed to show that *Rana esculenta* is negatively phototropic and LOEB considered this probable. PLATEAU ('89, p. 82), however, found that *R. temporaria* is positively phototropic. PARKER ('03, p. 30) also found that *R. pipens* is positively phototropic, not only in the normal condition, but also when the eyes are removed. Later Miss TORELLE ('03, p. 487) discovered that *Rana virescens* and *R. clamata* are positively phototactic at ordinary temperatures, but that raising the temperature to 30° C. accelerates the rate of positive response, while a lowering of the temperature to 10° C. produces movements away from the light. KORANYI ('93, p. 6) says that microscopical changes in the retina of *Rana* may be effected by the exposure of the skin, as well as the eye itself, to light.

The results of experiments on Urodeles seem to be more uniform than those of experiments on the Anura. CONFIGLIACHI and RUSCONI were probably the first to point out that some of the Urodeles are negatively phototropic. They noted that *Proteus* always retreats towards darkness. These investigators thought the effect upon the skin, rather than upon the eyes, caused the animals to seek darkness. GRABER's ('84, p. 96) experiments on the young of Triton, in which he found them negatively phototropic, even when their eyes had been removed and their heads covered with black wax, led to the assumption that the skin can be stimulated by light. DUBOIS ('90, p. 356) who covered the eyes with gelatine and lampblack, concludes that *Proteus* distinguishes light from obscurity both by the eyes and skin, but that the dermatopteric sensibility is far less powerful than the ocular sensibility. WHITMAN ('98, p. 302) says of the young *Necturus*: "It is interesting to see how little the eyes are depended upon in finding a piece of meat. A bit dropped in front of a young *Necturus* receives no attention after it reaches the bottom. An object must be in motion in order to excite attention, and it is not generally the moving form that is directly perceived, but the movements of the water, traveling from the object to the sensory hairs, are felt, and in such a way as to give the direction of the disturbing center with most surprising accuracy. If a bit of beef is taken up adhering to the point of a needle and held in the water, the vibrations imparted to the needle by the most steady hand will be sufficient to give the animal the direction. If the meat falls to the bottom,

and the needle is held in place, the animal approaches the needle and tries to capture it without paying the slightest attention to the meat lying directly below. If, after the meat has fallen, the needle is withdrawn and touched to the surface of the water behind or at one side of *Necturus*, it turns instantly in the direction of the needle not because it sees, but because it feels wave motions coming from that direction. Long experience with *Necturus*, and with many of its nearer allies, enables me to speak very positively on this point. When it is remembered that in the higher animals the direction of sound waves is given by the auditory sense organs, which are primarily surface sensillæ homologous with those in the skin of *Necturus*, it may not seem so strange that the animal directs its movements in the way described. *Necturus* can see, but it can feel (perhaps we should say hear) so much more efficiently that its small eyes seem almost superfluous."

All the facts thus recorded seem to show that the eyes of the young *Necturus*, as well as those of many other Urodeles, are not highly functional structures, and that when the animal is deprived of their use the dermatopteric sense adequately compensates for the loss.

As PARKER ('05, p. 418) has well said, "The ability of the spinal nerve terminals to be stimulated by light may now be said to be established for certain fishes, amphibians and reptiles; and this fact is not without interest in connection with the theories of the origin of the vertebrate retina."

The many attempts to explain the inverted position of the vertebrate retina early led to hypotheses by LANKESTER ('80), BALFOUR ('85) and BEARD ('88) that the eyes are structures which have been evolved from light perceiving organs which were at one time located in the unclosed neural plate. BISCHOFF, KÖLLIKER, HIS, VAN BENEDEN and others long since observed in mammals a very early appearance of the optic vesicles. HEAPE ('84) observed the optic vesicles in the mole when the neural folds were widely open in the head region. KEIBEL ('89) later observed that in the guinea pig a like early differentiation of the optic vesicles occurs. WHITMAN ('89) discovered that in *Necturus* there is a very early appearance of the eye, "its basis being discernible as a circular area long before the closure of the neural folds of the brain."

No one, however, had ever shown that the optic vesicles were present in the neural plate at the time the neural folds first appear,

until the writer ('93) showed that in *Rana palustris* the *Anlagen* of the optic vesicles not only appear as a pair of pigmented areas, but that these areas are made up of pigmented columnar cells so different from the cells in the remainder of the neural plate that there could be no reasonable doubt of their being specially differentiated areas. By following these areas step by step during the period of closure of the neural folds it was definitely established that these areas formed the bases of the future retinae.

Shortly after the publication of the writer's observations LOCY ('93) found a series of depressions in the unclosed neural plate of certain Elasmobranchs which he thought represented paired sensory structures, probably, of a visual character.

In a word, it may be said that the evidence has been slowly accumulating from the morphological side in support of the hypothesis that the retina belongs to the cutaneous sensory system.

The evidence from the physiological side is equally confirmatory. PARKER ('05, p. 419) who has recently carefully reviewed the literature states that "This sensitiveness of the vertebrate skin to light is probably a remnant of that primitive condition from which the lateral retinas were derived, and possibly served as a basis from which the temperature terminals of the skin in the higher vertebrates developed."

In conclusion, then, one may say all the evidence goes to show. as JOHNSTON ('05, p. 241) has well stated, that "the retina belongs morphologically, as well as physiologically, to the cutaneous sensory system."

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RECENT STUDIES UPON THE LOCOMOTOR RESPONSES OF ANIMALS TO WHITE LIGHT.

BY

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During the last few years attention has been given to the light reactions of nearly all the large groups of invertebrates. The sudden appearance of data upon the photic responses of animals differing greatly in habits and in mechanism of locomotion has naturally resulted in a variety of opinions as to the proper classification of their orientations. The wide latitude as to precision of light control, amount of quantitative experiments, emphasis laid upon the mechanism of locomotion, and the like, exhibited by various investigators, has increased this diversity. Nevertheless recent discussions make good the claims of trial¹ and phototaxis² as two mutually exclusive but closely associated categories within which most features of animal light response may find a place. Papers not concerned with these subjects may in most cases be best considered in relation to the animal group to which they refer. The period to be given attention extends from the year 1900 to 1907 inclusive.

PHOTOTAXIS.

Although some of the postulates of the mechanical phototactic theory of a few years ago have not survived, there can be no doubt that most of the animals to which it was applied have one characteristic in common. They align with the light by a movement whose direction has a definite relation to a localized photic stimulus. Some recent papers may help us to determine the accuracy and speed with which they align and the relation of bilateral symmetry to the procedure.

HARPER's accounts ('05, '07) of the behavior both of the earthworm *Perichæta* and the larva of the insect *Corethra* have an important bearing upon the questions just suggested. The earthworm is found to react by the trial method if the light be of low intensity. Under greater illumination exploring movements in the direction not aiding orientation gradually disappear. The animal then aligns itself with the light by a few quick turns. This procedure illustrates the fact that the turning provoked by localized stimulus may consume an appreciable amount of time and may consist of a series of movements. It might be mentioned here that PARKER found *Planaria* to orient phototactically by a curved course of some length.

The larval *Corethra* has a discontinuous jerky locomotion. The successive advances are invariably in a path bending towards the source of light. Neverthe-

¹ The expression "trial and error" may be shortened to "trial" because the second term is implied in the first.

² The view of RADL is here adopted that the older term phototropism should be applied to all motor responses of animals which are produced by light as does geotropism to those produced by gravity, chemotropism to those produced by chemical stimuli, etc.

less they do not produce alignment because the animal always curves too far. In spite of its zig-zag path the larva always responds to the greater illumination of one side by turning in that direction. Alignment is defeated by a peculiarity in the method of locomotion.

HARPER points out the inconsistency of applying to *Corethra* the mechanical theory of phototaxis as it was stated by DAVENPORT for the earthworm. It was the suggestion of that author that orientation would result in a simple and mechanical way if we suppose, first, that light directly modifies the tonus of the muscle and, second, that optimal illumination gives the highest tonus. Under these conditions the side of the animal towards the more nearly optimal light would contract the most and the animal thus turn towards optimum. In spite of the fact the *Corethra* is a worm-like larva, the theory cannot apply to it because it contracts on the side away from the optimum.

RADL ('03) is the author of the most complete account of phototaxis that has yet appeared. A considerable part of his monograph is occupied by his own study upon insects and other arthropods. A variety of interesting facts have been brought to light. Butterflies of various families may be found toward sunset perching upon flowers with body pointed away from the sun, wings outspread and head raised or depressed so as to bring the back of the wing as nearly perpendicular as possible to the sun's rays. In the middle of the day certain species close their wings and align with the light. In general RADL says: "Some butterflies so orient with the sun's rays that in weak sunlight they expose the greatest possible surface, in strong sunlight the smallest surface of the wings." He leaves the explanation for later investigators. BOHN has described similar orientation in butterflies. Certain dragon flies persistently orient with the right side to the sun. Midges have a curious way, little understood, of flying in a circle or spiral within a small area at some point near a light. This place may be forsaken and a new position taken up, only to repeat the previous behavior. Actively moving Cladocera are found in dense swarms within the free spaces among the algal clumps in fresh water ponds. There is a clear band several centimeters wide between them and the shore. The face of the moving mass is clean cut and follows every irregularity in the lateral surface of the algal mass. A similar condition of things is not obtained in the laboratory and an explanation has not yet been discovered.

RADL also found that many aquatic arthropods show an orientation to the light divorced from their locomotor response. *Daphnia*, for example, regularly orients with its back to diffuse or direct sunlight, while at the same time moving about in a non-directive way. It will turn its back upward if the light be made to come from above or downward if the direction be reversed. Animals were kept in an inverted position for two weeks in this way with no diminution in the precision of the response. He also obtained that locomotor reaction described by DAVENPORT, YERKES and others, for Crustacea, which is characterized by rapid orientation to light and a symmetrical arrangement of the body in relation to the direction of the rays. The conditions which determine whether orientation with back towards the light or with orientation with long axis in line with the light and accompanied by locomotion, shall control the animal have not been determined.

Other peculiarities regarding the relation of body to locomotion have been recently described for arthropods. Pycnogonids (COLE '01) go towards the light with the head leading provided they are crawling, but swim toward it with the abdo-

men in advance. *Palæmonetes* larvæ swim with abdomen toward the light. LYON ('07) caused them to move head first towards the dark by diluting the seawater.

A considerable part of RADL's investigation, like that of LOEB and LYON at an earlier period, relates to the movements of insects and other arthropods placed upon disks rotating in various planes. Some animals remain standing upon disks and automatically turn their heads to maintain their orientation to the light. Some, if upon a slowly moving horizontal disk, keep in such a position that they do not lose their orientation to light or to the surrounding fixed environment. The relation of these reactions to the explanation of light responses can best be made clear after recalling a view expressed by LOEB ('07, etc.). Binocular vision, he believes, is phototactic because a pair of eyes are always placed symmetrically in respect to the center of the field of vision by virtue of their adjustment so that it will fall upon the middle points of their retinas. RADL conceives phototaxis as a response to localized stimulus resulting in symmetrical adjustment. He believes binocular vision is phototactic in his sense of the term phototaxis. At the same time he acknowledges that such phototaxis has two novel elements: namely, the substitution of the varied field for a simple source of light, and the orientation of organs instead of the whole body. In regard to the former, he admits that there has not as yet been brought forward any series of phototactic reactions to fields of gradually increasing complexity as a proof that orienting to them is essentially the same as orienting to a simple source of light. RADL together with LOEB and LYON have found that orientation of eyes as well as head are shown by compensatory movements to be very common in insects. So frequently does it occur that RADL is led to say that the essential of arthropod phototaxis is the orientation of the eyes, and that the adjustment of the body follows only at times, and is of secondary importance.

HADLEY ('06, '06a) has recently shown that young lobsters keep a constant position relative to the bottom while in moving water. This is partly due to orientation toward the fixed field about them. The optical portion of the process may be directly compared with compensatory locomotion upon a revolving disk. Mechanical compensatory movements due primarily to light, and resembling those of the young lobster, are described by LYON ('04) in a study of the rheotaxis of certain fish. LOEB ('07a) finds that marked compensatory head movements are made by the reptile *Phrynosoma* upon the revolving disk. His experiments show them to be in part due to optical reflexes. It is evident that the compensatory movements of vertebrates, in so far as they are optical in origin, have in them the qualities of similar arthropod movements. If the term phototaxis may be applied to the binocular vision of arthropods, it also can rightly be used for vertebrates. Such a statement needs the corollary that phototaxis probably expresses only a tithe of the nervous activity involved in the binocular vision of the vertebrate.

There has been presented a fair illustration in the variety of locomotion which may result from the response to localized stimulus as described by recent authors. We are therefore in a position to consider whether these different procedures have anything further in common. Opposite conditions in the complexity of aligning movements are illustrated by the earthworm and flatworm as compared with certain crustaceans, as *Daphnia*. Some animals also stand in contrast with *Daphnia* because of the greater irregularity of their course to or from the light. Thus in *Corethra* peculiarities of locomotor mechanism produce a zigzag course. In spite of the great variety which these animals just mentioned show in their accuracy of

orientation because of differences of locomotor mechanism and other factors, they have in common, that they align with the light more or less accurately as a result of its differential effect upon the opposite sides of a bilateral symmetrical body. There is thus a response to localized stimulus. The available evidence goes to show that animals responding to localized light stimulus have in general this same character. Even the bell-shaped jelly-fish and a spherical form such as *Volvox* come within the category inasmuch as radially symmetrical animals must be also bilaterally symmetrical. In the further use of the term phototaxis we shall therefore imply alignment by the differential effect of light upon the sides of bilaterally symmetrical organisms.

JENNINGS attaches little value to this view of phototaxis because it does not pretend to seek a full explanation of things as did the old mechanical theory. He says, "In order to retain any of its value for explaining movements of organisms, it would have to hold at least that the connections between the sense organs and the motor organs are of a perfectly definite character so that when a certain sense organ is stimulated a certain motor organ moves in a certain way." It is to be granted that there is little of an explanatory character in phototaxis as defined above. Nevertheless it has the value which attaches to all categories. It represents a certain stage in the classification of facts, and is a unit of behavior which will simplify further attempts at analysis in the same direction.

LOEB and RADL rightly claim that there is a graded series between such a locomotor response as we have just defined and the training of the two eyes of a vertebrate upon any object. The comparative anatomy of various types of eyes, as well as those experiments upon light response which bear upon the subject, strongly indicate that there is also a graded series between orientations to a single source and those to a varied field. The question of the practicability of applying the term phototaxis, which originally referred to locomotor responses of lower animals alone, to a series including the orientation of eyeless animals on the one hand and of the vertebrate eyes upon the other, is simply one of convenience in terminology. In this paper it will be used in the wider sense.

Perhaps no contribution has appeared which shows more clearly the relation between phototaxis and the general nervous activity of an animal than does the study by HOLMES ('05a, '07) of the reactions of the insect *Ranatra* to light. The behavior of the animal is dominated to a surprising degree by photic stimuli. It is marked not only by phototaxis of the body but its eyes and breathing tubes sway towards an alignment with the light even when the animal is not engaged in locomotion. If various parts of the eyes be blackened there results the phototactic response which we would expect if the part of the environment dark to the animal were really devoid of light. HOLMES points out that this slavish and mechanical response is probably due to simple reflexes.

But the behavior of *Ranatra* also reveals more complex nervous processes existing side by side with phototaxis. Hemisection of the brain destroys light response almost completely. Therefore it is probable that the crossing optic fibers in the brain are part of the reflex arc. A number of stereotyped procedures such as hunting food and cleaning the body may inhibit phototaxis. Of especial interest is the result of blackening all but a small posterior portion of one eye. There is a marked disturbance of orientation as one would expect. In spite of this fact, the animal in time learns to move towards the light quite accurately. HOLMES argues that no simple reflex can explain orientation under these conditions.

The first experiment definitely directed to determining the relation of phototaxis and the image-forming power of the eye is described by Parker ('03a). He made use of the positively phototactic butterfly, *Vanessa*. The animal was placed in such a position between a window and a candle that the intensities of light from the two sources were equal where they fell upon the animal's body. Under these conditions *Vanessa* flew towards the window, thus demonstrating that it can distinguish between the size of luminous fields. Phototaxis is preceded by a choice of the field to which it orients. The experiment, as PARKER points out, furnishes an answer to the query why positively phototactic winged insects do not fly towards the sun. They seek instead the larger mildly illuminated patches upon the earth's surface.

COLE ('07) employed PARKER's test upon a number of terrestrial animals and thus increased our knowledge as to the relation of phototaxis and the power of forming primitive images. The animals were placed perpendicularly to the line joining two parallel screens and equidistant from them. The light given off by the screens per unit surface was inversely proportional to their size. Therefore the total light intensities of their surfaces were equal. The dung worm *Allolobophora*, the insect larva *Tenebrio*, the cockroach *Periplaneta*, the European garden snail *Helix*, and the blinded cricket frog *Acris* did not give a greater number of turnings to one field than to the other. On the other hand the flatworm *Bipalium*, and the small crustacean *Oniscus* showed some little power of discrimination. *Vanessa*, *Ranatra*, and two species of frogs with eyes intact distinguished readily between the screens and always oriented to a particular one of them.

A discussion of the relation between perception of detailed images and phototaxis appears in a recent work upon vision by NUEL ('04).

TRIAL.

JENNINGS was the first to apply the idea of trial, long recognized for vertebrates, to invertebrates as well. We shall consider the papers on this subject relating to the earthworm by PARKER and ARKIN, SMITH, ADAMS, HOLMES and HARPER before turning to the protozoan studies of JENNINGS.

The methods used by SMITH ('02) in studying the earthworm are valuable in giving, as it were, a birdseye view of its activities in light of rather weak intensity. She devised a means of plotting upon paper the path of the worm for a considerable distance. Exploring movements were shown by spurs upon the line indicating the animal's course. When worms are started with their bodies perpendicular to horizontal light, they go in various directions, varying from directly toward to directly away from the light. In the great majority of cases the course is obliquely from the light. Exploring movements are especially common when the anterior end of the worm encounters stronger illumination or an unfavorable surface. Often they are preceded by a recoil. Although the fact is not emphasized by the writer, her diagrams show that exploring movements toward the light are not followed up so frequently as those away from it.

We must turn to HOLMES ('05) for the application of the trial idea to the worm. He makes the statement that the first effect of moderate light upon the earthworm is the production of exploring movements, of the anterior end, haphazard as to direction, with possibly a few more away from the light than toward it. The second effect is to check the movements toward the light. As a result the animal

becomes roughly oriented negatively to the light. He calls the process "the selection of random movements," and points out that it resembles the trial method of higher animals, with the reservation that there is here no learning by experience.

HARPER ('05) gives us a very reasonable explanation as to the mechanism of the exploring movements. He finds that the extension of the anterior segments of the worm presents more fully to light certain cells, probably photoreceptive, which lie near the dissepiments. An animal must extend its anterior end well out in a certain direction, therefore, before light can produce inhibition of further movement.

PARKER and ARKIN ('01) had published, previously to the appearance of the papers by SMITH and HOLMES, an account of the orientation of the earthworm *Allolobophora*. Their method of procedure was to tabulate the movements of the anterior end in a large number of trials made upon individuals placed transversely to the direction of the light. There were 66 per cent of movements straight ahead, 4 per cent toward the light, and 30 per cent away from it. The view was taken that the 4 per cent toward the light indicate disturbing influences of other stimuli, and so that it is probable that 4 per cent of those away from the light have a like cause. The remaining 26 per cent of those away from the light indicate a tendency of the animals to orient to the stimulation of light in the phototactic way.

Another test of photic response was devised which gave very suggestive results. Light was thrown perpendicularly at different times upon the anterior, middle, or posterior thirds of the body. The percentages indicating the orienting effects are 10.2, 2.4 and 1 respectively as compared with 26 per cent of turns from the light when the entire body was illuminated. It is evident that the condition of the trial reaction as described by HOLMES is present when only the anterior end is illuminated. Yet if the rest of the body be also exposed to light the orienting response more than doubles in amount. The experiment suggests the unreasonableness of thinking that this elongated animal, sensitive to light along its whole length, should make no use, in its orientation, of that wide difference of intensity which must often exist between its opposite ends.

A recent experiment by COLE ('07) suggests that the importance of antero-posterior differences of intensity could be found if a partial shadow were cast upon the earthworm's anterior end when in a field of horizontal light perpendicular to the long axis. A difference of illumination of the two sides of the anterior end would exist such as would fulfill the conditions for a turning by the trial and error method. At the same time if the difference in intensity of the anterior as compared with the posterior end of the animal were effective we should expect a movement straight into the shadow.

ADAMS ('03) applied the methods of PARKER and ARKIN to *Allolobophora* with the intention of determining the effect of twelve different intensities of light ranging from 192 candlemeters to .012 candlemeters. At 192 candlemeters there were 41.5 per cent negative movements which showed the orienting influence of light. At 8 candlemeters there was an increase to a maximum of 59 per cent of negative reactions. The percentage decreased gradually to 3 per cent at .012 candlemeters. The very low intensity of .0011 candlemeters was found to produce a preponderance of positive movements. This increasing proportion of precise movements away from the light tallies in a general way with the behavior of *Perichæta* when it forsakes all non-orienting movements in strong illumination. But *Allolobophora*

shows a slight falling off of direct reactions from 8 candlemeters up to 192 candlemeters instead of the uniform increase seen in *Perichæta*. Of course it cannot be expected that the different genera of worms used by the two experimenters should agree in the details of their reactions.

The trial method as described by HOLMES with its production and checking of varied movements is confirmed by HARPER as far as *Perichæta* is concerned, and it is hinted at by SMITH. The observations of PARKER and ARKIN do not invalidate its occurrence, because we do not know that they attempted to record a checking of exploring movements. There is, therefore, little doubt that there are both phototactic and trial phases in the behavior of worms, as well as that dependent upon the relation of the stimuli antero-posteriorly along the animal.

Only those parts of JENNINGS' study ('00, '04, '05, '06, '06a) of Protozoa need be considered here which refer to the method of orientation to light and to his conception of the trial reaction. He found that alignment takes place by a swinging of the anterior end of the animal away from a structurally defined side due to an unfavorable change of intensity. This he terms an avoiding reaction. In case it is initiated by an abrupt entry into a field of perpendicular light of unfavorable intensity there is usually a quick return to the ordinary spiral course. The turn often serves to take the animal out of the unfavorable field. If it does not accomplish that end the process will be repeated until it gets out or becomes acclimated to the new conditions. If at any time it blunders into a field of favorable intensity it is evident that it will be held there as in a trap. A second variety of the reaction usually occurs if the animal be moving at an angle with horizontal light. The beat of the cilia which produced the swing is then likely to continue longer and the anterior end move around a larger circumference than usual. If forward motion be entirely stopped it may describe the surface of a cone or disk by whirling on its posterior end. Some part of the curve which is traversed by the anterior end of necessity leads into increasingly favorable light intensity and the stimulus for the swinging, which was an unfavorable change of illumination, is thus removed. The ordinary spiral course is resumed but the direction is now more nearly in line with the light. By a series of such turns, often very close together the protozoan soon becomes directed as nearly toward the light as its spiral motion will permit.

The following definition of trial is given by JENNINGS ('06) which he applies to the protozoan methods and to that of the earthworm as well. "The organism performs varied movements, some features of which are not determined by the localization of the stimulus but by other factors; it then continues those movements which bring it into or toward a certain condition; this condition usually being a greater or less action of the stimulating agent as the case may be."

This statement of trial differs from that of HOLMES in two of its features. JENNINGS does not confine varied movements to such as are produced by an unfavorable change of illumination. A comparison of earthworm and protozoan varied movements will show whether the latter may be considered due to a change of light intensity. The exploring movements of the earthworm constitute its varied movements. They may be clearly distinguished from the movements which carry the animal along because they are confined to the anterior end of the body. The avoiding reaction of a protozoan, upon the contrary, may consist of ordinary locomotor movements modified by a swing from the structurally defined side due to an unfavor-

orable change of illumination. It is the avoiding reaction which constitutes the varied movement of the protozoan. All components of its motion are not evoked by change of light intensity. Then why refer in a definition of trial to the method by which the varied movement is produced? HARPER ('07) in a recent paper gives a reason. There are a great number of irregular movements, especially among lower animals, which by carrying their possessor into a large number of regions help them better to test the surroundings. Such, among others, are the spiral movements of the protozoan not involved in the avoiding reaction, and certain writhings of insect larvæ. These do not aid in orientation to light and in most cases do not result from unfavorable change of illumination. The trial reaction is therefore to be considered as resulting from varied movements produced in whole or in part by change of light intensity.

JENNINGS does not make the checking of some varied movements an essential part of trial. He says merely: "Movements are continued which bring the animal into or toward the favorable condition." A moment's consideration of the method of the trial procedure in Protozoa makes the reason for his attitude clear. There is first an increase of the ciliary stroke producing the movement from a structurally defined side. When the anterior end of the animal in pursuing the enlarged spiral is brought into more favorable light intensity the increased vigor of stroke disappears. The process is not a checking of any movement by unfavorable illumination.

The orientation of protozoan and earthworm plainly have some differences. Yet the two have sufficient in common to warrant their inclusion within a single category. Orientation by trial then consists in the production of varied movements which are at least in part produced by an unfavorable change of illumination, and the following up of those leading towards favorable illumination.

JENNINGS' account of protozoan behavior to light was soon followed by a paper from MAST ('06) upon the protozoan, *Stentor*. As the latter says: "JENNINGS laid particular stress on the detailed movements of the individuals while I directed most careful attention to the regulation of the stimulus."

One carefully planned device which he employed gave him a graded field of vertical light. When subjected to it, *Stentor*, which is negatively phototropic, becomes directed in some path which does not lead into greater intensity. That is to say, it becomes oriented to such an extent that its head points within 90° to one side or other of the line which would carry it most directly toward the dark.

MAST raises a doubt as to whether the avoiding reaction of Protozoa is a trial response at all. His examination of the threshold of light stimulation for different parts of a *Stentor* shows that the peristomal region is probably much more sensitive than the rest of the surface. Therefore light stimulus is most likely to be received in this region. Inasmuch as the animal turns from the peristomal side in an avoiding reaction it is giving a definite response to a localized stimulus just as truly as is an insect which upon one eye being blinded turns away from the remaining one. The localization of light sensitiveness and the turning from the localized area cannot as yet be considered as an established fact.

Does the protozoan show an alignment of a bilaterally symmetrical body to the light? It does so only imperfectly because of its spiral movement. Inasmuch as many phototactic animals only roughly approximate a straight course because of peculiarities in their locomotor mechanism, such a condition would not prevent

the regarding of protozoan orientation as phototactic. There is a consideration, however, that would do so, even though it were proven that a response to localized stimulus occurs. There are no paired bilaterally symmetrical sensory areas through whose unsymmetrical stimulation orientation is accomplished.

DIRECTION VS. INTENSITY.

RADL ('03) makes the statement that from a physio-chemical point of view there can be no question as to whether intensity or direction is the primary factor in the action of light upon an animal. The amount of change produced in the protoplasm by light is due to the amount of energy given up by the light, and that in turn is a function of intensity, not of direction. That this view does not exhaust the question is shown by a test which HOLT and LEE ('01) applied to the protozoan *Lyncæus*, in imitation of the earlier experiments by COHN. Their apparatus consists of a wedge-shaped tank containing dilute india ink suspended over an aquarium. Light from above produces in an imperfect way a field graded in intensity from one end of the aquarium to the other. By varying the angle of incidence upon the prism the light is given an oblique direction within the aquarium and the gradation of the field is little changed. *Lyncæus* aligns itself with the light, and goes slavishly into either greater or less intensity according as the rays slant in the one or the other direction. This kind of reaction had been previously used as an argument that direction is the essential factor of light response. HOLT and LEE applied in explanation of the reaction VERWORN's suggestion that if an animal always turned toward the shaded side of its own body it would of necessity align with the light. Thus *Lyncæus* is forced into either light or dark areas while responding in an unvarying way to the difference of intensity upon the sides of its body. Although HOLT and LEE have thus explained the behavior of the animal satisfactorily by means of intensity changes, they did not settle the question of the relative merits of intensity and direction.

We owe to MAST ('07) the first conclusive proof that orientation is due primarily to intensity. He used for his purpose the colonial protophyte *Volvox*. An individual was first illuminated by two like pencils of light. As a result it took a course intermediate between them. Then without changing the direction of either beam one of them was modified in intensity. The organism now changed its orientation, bending its course somewhat toward the beam that had become relatively stronger. COLE ('07) illustrated the same point in another way upon the two worms *Allolobophora* and *Bipalium*. A partial shadow was cast upon the anterior end of a worm which has been pointed toward the nearly horizontal light. The creature in spite of the fact that it is negatively phototropic went into the shadow, thus moving almost directly toward the source of light. Serpulid larvæ, though phototactic, were found by ZELENY ('05) to go into greater light intensity whether it led them in the direction of the light or not.

It is not necessary to seek for further evidence that light produces stimulation through variations of intensity. Direction plainly affects the intensity of light upon the body or the retina by the casting of shadows or by the complications introduced through eyes of varying position and visual angle. TORREY ('07) has recently recalled to mind the view that light may possibly show an orienting effect dependent upon direction in a way analogous to the action of an electric current. Such a theory would not explain the orientations of *Volvox* and *Allolobophora*.

PROTOPHYTA.

MAST ('07) has produced a well rounded and thorough piece of work upon the photic reactions of *Volvox*. Although the form is classified as a plant its locomotion is of a protozoan type and so is of interest here. The first part of his report gives an analysis of its curious method of locomotion. His apparatus is carefully planned and the methods applied to determining its behavior are various. Equal attention is given to the reactions of segregated individuals and of large numbers taken together. *Volvox* is found to orient by phototaxis, although through a peculiarity of its locomotion its path is at a slight angle with the light. The light response is analyzed into a series of avoiding reactions of the individuals comprising the colony. Various factors such as previous condition of illumination, the stage of development of the individual, etc., are described as modifying the light reaction.

COELENTERATA.

Gonionemus is an interesting object of study as a type of the primitive and unique group of the jelly fishes. YERKES ('02, '03a, '04, '06) contributed a paper upon its light reactions in a series treating of different phases of its nerve physiology. MORSE ('06, '07) has also devoted some attention to the subject.

According to YERKES ('03a) *Gonionemus* is decidedly phototactic under certain conditions of illumination. The response to localized stimulus can be readily seen if the individual in a negative condition happens into a band of light of graded intensity such as may occur at the edge of a shadow. The side of the bell toward the light which is most intensely illuminated contracts most strongly and the animal thus turns back into the shadow. The juxtaposition of contracting and stimulated regions results in a localized response reduced very nearly to its simplest terms. MORSE has confirmed YERKES in the occurrence of directive response by observing single medusæ in various conditions of illumination.

A marked photokinetic effect occurs. As LOEB earlier found for *Planaria* the medusæ will collect in a shadow because as soon as their active movements bring them there they come to rest. This method of non-orienting response to intensity of illumination has been termed negative photokinesis. It has been already stated that a graded field at the edge of a shadow may produce a phototactic orientation of stragglers which directs them back into the shadow. Thus non-orienting light response and phototaxis coöperate.

PLATHELMYNTES.

Three investigations have been recently published upon the flatworms by PARKER and BURNETT, GAMBLE and KEEBLE and WALTER.

PARKER and BURNETT ('00) so planned their experiments upon the negative *Planaria* as to determine the importance of the eyes in orientation, and to show the relative importance of light as compared with other factors in locomotion. Single animals were placed at the center of the horizontal surface marked with a circular scale and directed toward the zero point. The angle at which they emerged was recorded, as well as the time consumed in the trip. If individuals with eyes were started toward the light it was found that they would, on the average, bend 78°

toward the right or left. Animals in a healthy condition, but with head cut off, showed a directive effect by an average bending of 57° . In case the initial direction coincided with that of the light the deviation from a straight line dropped to 24° for a normal animal and 35° for those without eyes. The conclusion is that phototaxis is only in part due to the eyes.

The amount of non-directive wandering which takes place was learned from the angle obtained under vertical light. Animals with eyes wander on the average 27° . The bending of 78° by animals headed toward the light must be discounted by this much to obtain the directive effect of light upon them. The course away from the light with 24° of wandering has a turning of only 3° , due to the directive action of light. The results of the comparison of the undirected with the directed course of *Planaria* are in point with the criticism made by TORREY ('07) upon JENNINGS' view of the manner in which animals may move forward after they have once become oriented. The latter believes that a straight course may be regarded as due in part at least to a lack of any stimulus of light or any other agent which would tend to turn it. TORREY takes the position that the straight course may be due to balanced rather than to non-stimulation. As a matter of fact, we have seen that *Planaria*'s course from the light is influenced only slightly by the light.

Convoluta, to which GAMBLE and KEEBLE ('03, '03a) gave their attention, is a sedentary planarian containing a large amount of chlorophyl. The animal gives a positive response in strong illumination which is markedly greater or less depending upon whether the bottom of the aquarium is white or black. The conditions of tonus found in this creature are peculiar, very likely because of the presence of chlorophyl in its body. If kept in darkness for a while its muscles become contracted and its movements sluggish. Very strong light produces a similar effect except that the animal is now unusually susceptible to being broken to pieces if handled. *Convoluta* lives within the tide lines and periodically moves to the surface of the sand. The changes in tonus give GAMBLE and KEEBLE an explanation of this procedure.

The study of planarian light reactions by WALTER ('07) is one of the most extensive and many-sided contributions that have as yet appeared upon the light-reactions of any group.

A comparison is made between representatives of several genera in regard to nine different varieties of response which he distinguishes in the animals. Diagrams are given of typical paths followed by the various species if allowed to roam in an aquarium until they come to rest. WALTER says of these, "It may be affirmed that the generic differences are so pronounced that one could take a miscellaneous unidentified assortment of such records and correctly assign the great majority of them to the proper genera." Two species of one genus show a nearer relationship in behavior than do the different genera.

Among the conditions of illumination which were applied to the worm are a series of intensities of non-directive vertical light, including zero intensity, changes in the strength of the entire field of non-directive light, two adjacent non-directive fields of differing intensity, directive light of constant and of varying intensities. Animals in the dark make many double turns which are termed "indefinite" as they evidently are not of orienting value. In non-directive light they are replaced by single turns. The stimulating effect of simultaneous change of intensity over the entire animal varies with the rapidity of change. Decrease of illumination is more of a stimulus than an increase.

A large number of observations upon the effects of other tropisms, physiological states and various internal factors are recorded. For example, some individuals were found to change from the usual response of the species for a time and then to return to it.

By a certain arrangement of conditions it is shown that negative photokinesis is overcome by phototaxis. The tendency to wander may result in many excursions contrary to the phototactic influence. This increases the effectiveness of negative photokinesis by bringing the animals into dark regions to which they would not come through phototaxis.

CRUSTACEA.

The photic reactions of crustaceans have received much attention. Their phototaxis is characterized by quickness of alignment with the light and straightness of course. Photokinesis is often strikingly marked. One is especially impressed in looking over the papers upon the group by the variety of ways in which a reversal of phototaxis has been produced.

TOWLE ('00) found that the positive Cypridopsis could be readily made negative by squirting it through a pipette. Negative animals could less readily be turned to positive by the same means.

In a series of papers upon entomostracan light reactions by YERKES ('00, '03) a similar condition of things is described for Cypris and Daphnia. Cypris is made positive in this way, and Daphnia faintly negative. In the latter animal it could not be determined whether the opposite effect could be produced, for the negative condition was at the best very weak and transitory. YERKES believed that in general the reversal most readily effected is from the less to the more common reaction for each species. There is some probability that the stimulus producing the change is thigmotactic inasmuch as according to PARKER's observation, the crustacean *Labidocera* though affected in like manner to these others when squirted through a pipette, is not influenced as to its light response by vigorous shaking.

YERKES attempted to find whether increase of intensity calls forth greater accuracy of phototactic response. The question was answered by observing the duration of trips of constant length made by *Daphnia* and *Cypris* under various conditions of illumination. There occurred a marked shortening of the period occupied by a trip if the illumination was increased. YERKES believes this partly due to a straightening of the course and therefore to more accurate orientation. The difference between its phototaxis and that of *Corixa*, therefore, consists only to the degree of accuracy of the orientation. *Daphnia* was found to recoil and turn back into the light if its head came into a shadow somewhat as in the avoiding reaction of Protozoa.

YERKES has been able to obtain a physically perfect graded field of vertical light by means of a lens consisting of the segment of a cylinder. All light which passes through the bottom of the aquarium is deflected away by a mirror, thus avoiding reflected light. A *Daphnia* placed in the apparatus goes obliquely upward toward the lighter end at an angle of 45° ; it is evident that this is partly due to an attempt at phototactic alignment with the vertical light. The significance of the horizontal component of this motion is not stated.

Daphnia does not seek an optimum but moves unhesitatingly into the most intense illumination it can reach. The harmful effects of strong light are shown

by jerky and disorganized movements. PEARL and COLE ('01) have described a like photokinetic effect in a variety of animals which they subjected to the light of a projection lantern. A leech, a nemertean worm and a small crustacean are rendered especially active by strong light until they show exhaustion by sluggishness and insensibility to tactile stimuli. HOLMES ('05a) finds that *Ranatra* acts like *Daphnia* in strong light, yet when it has been in the dark for a time it is not only sluggish but negative. The amphipod *Orchestia* which lives under drift seaweed is negative for a time when exposed to daylight, but turns positive much as does *Ranatra*. The beach flea *Talorchestia*, though a nocturnal animal, gives a positive response as strong as any that has been recorded. *Ranatra* also responds in a positive way with great vigor. The positivity of these dark-loving animals requires explanation.

Increase of temperature hastens a change of *Ranatra* in a positive direction and accentuates the positive response when it is already present. Dipping into water gives a negative reaction which is probably a contact effect. HOLMES ('01) discovered that the immersion of certain terrestrial amphipods will also effect a reversal.

Labidocera was found by PARKER to behave toward light differently from *Daphnia* and *Ranatra*. It reacts positively in diffuse light, but turns strongly negative in direct sunlight. He cites a number of similar cases. The possible adaptive value of the reaction does not need to be pointed out.

SMITH ('05) brings forward a reasonable explanation of the gradual change of sense of response in a number of crustaceans, when subjected to a marked increase or decrease of illumination. It depends upon the fact that in *Gammarus annulatus*, as in many other crustaceans, the retinal pigment of the individual put from the dark into the light migrates distally at a rapid rate for about fifteen minutes, then moves more slowly for the remainder of an hour. This mechanism protects the more sensitive parts of the eye from over illumination. A large part of a group of animals subjected to strong light change their response within fifteen minutes. At the end of an hour nearly all will be positive. A possible relation between pigment migration and photic response is evident.

DIURNAL MIGRATION.

PARKER and ESTERLY contribute to the explanation of the movements of plankton crustacea and HARPER of insect larvæ from their nocturnal position at the surface of the water to greater depths during the daytime. PARKER ('02) concerned himself with *Labidocera aestiva*, a typical marine plankton crustacean. He first made sure that geotropism could not account for the migration by any reversal through the agencies of temperature and density. Weak illumination gave a positive response; daylight produced a negative reaction sufficiently strong to overcome the negative geotropism. He thus explains the migration: "Females rise to the surface with the setting of the sun because they are positively phototactic to faint light and negatively geotropic; they descend into deep water at the rising of the sun because they are negatively phototactic to strong light, their negative geotropism being overcome by their negative photopism. The males follow the females in migration because they are probably positively chemotropic toward the females."

A peculiarity of the method used by ESTERLY ('07) upon *Cyclops* consisted in subjecting animals after a long period in the dark to a series of intensities in various

orders of succession. By this means his records show the reaction of the animal to each intensity after exposure to each other intensity. This arrangement suggests a labor saving way of studying various kinds of previous stimuli upon light response. He finds that *Cyclops* is neutral to artificial lights of low intensity and negative to those of high intensity if it be subjected to them after confinement in darkness. Exposure for some time to light of any intensity makes it negative in all kinds of illumination. Especially interesting is the influence of light upon the geotropic response. Under illumination so diffuse as to be non-directive the animals are strongly positive in their geotropism. If light be removed they become negative. ESTERLY concludes that phototropism is of little importance in the diurnal migration in a direct way. Light, however, probably produces some photo-chemical change in the animal, as a result of which positive geotropism occurs during the day.

HARPER's ('07) work has to do with the insect larva *Corethra*. The animal is positively geotropic in strong light whether it come from above or below, and negatively geotropic in dim light. It is also distinctly phototactic. It is evident that the chief effect of the light upon migration must be due to its action upon geotropism. HARPER thinks that it is likely that while the animal would go down in the day and come to the surface at night obedient to geotropism it would also respond phototropically by collecting in well illuminated areas at whatever level it happened to be swimming.

There are several extremely interesting and rather lengthy quantitative studies upon the distribution of plankton in various American and European lakes of which a recent example has appeared in the work of JUDAY ('04). It is not advisable to discuss them here as their interest is chiefly ecological. It may be said, however, of JUDAY's work that it shows conclusively that light is a very important though by no means the only factor in diurnal migration. It brings to light the fact that the downward migration of plankton begins long before sunrise if not before midnight. The reason of this early departure from the surface is not forthcoming.

INSECTA.

In his paper on the light reactions of the pomace fly *Drosophila*, CARPENTER ('05) gives us one of the first general analyses, by laboratory methods, of the light responses of a winged insect. Like many Crustacea, *Drosophila* is strongly phototactic as well as photokinetic. Like *Daphnia* it will go into any strength of light without reversal. Very great intensity produces not only rapid movement but apparent loss of coördination. By shaking the jar containing the flies they are rendered negatively geotropic. It is a suggestive fact that as in the case of plankton crustaceans light may affect the geotropism while not acting directly itself. CARPENTER believes its effect is produced through a stimulating action much like that of the mechanical shaking.

MOLLUSCA.

FRANDSEN ('01), MITSUKURI ('01), WALTER ('06) and BOHN have given more or less attention to the behavior of gasteropod mollusks toward light within the period of this review. It would not be profitable to consider their papers since not only has there been a lack of an extended recent study of the group but there is also investigation under way upon their light reactions.

PISCES AND AMPHIBIA.

Certain work upon the compensatory movements of vertebrates has already been referred to while discussing existence of phototaxis in binocular vision. The attention of several workers has also been recently given to locomotor light responses of fishes and amphibians, in particular those dependent upon the light sensitiveness of the skin. Previously a few amphibians were known to possess this dermal function and blind newts of the genus *Triton* had been found to collect in the shade.

Two primitive vertebrates, *Amphioxus* and the larval lamprey, have been examined by PARKER ('05, '06) with the resulting discovery that both can perceive light through the skin. *Amphioxus* is phototactic and negatively photokinetic. The larval lamprey has these same characteristics. It is somewhat startling to learn that the latter animal orients even when the head is removed. The especial sensitiveness of the tail to light is correlated with a habit of burrowing head first until the rest of the body is covered. The earliest study of the orientation of blind fishes in response to light was made by EIGENMANN ('00) upon *Ambylopsis*. PAYNE ('07) has within the year repeated and extended EIGENMANN's observations. The animals gather in shade by some other process than direct orientation. They give a stronger response under vertical than under horizontal illumination. A photokinetic effect seems to be present along with movements suggesting discomfort. The experiments employed are simple and not devised to carry very far the analysis of the complex nervous activities of the animals.

PARKER ('03) demonstrates the occurrence of phototaxis for blind amphibians by means of frogs whose optic nerves have been severed. The animals can orient promptly, but only occasionally do they move toward the light. If the skin of a normal animal be covered orientation takes place readily by means of the eyes.

TORELLE ('03) concerns herself with the behavior of the frog without reference to the relative activities of eyes and skin. Orientation is tested in certain experiments by placing the frog in a box 12 in. long with a glass window 9 in. wide and 5 in. high. It may be objected to this procedure that the animal was presented with a pattern of light and shade whose image possibly covered only a portion of the retina at once. The only type of phototaxis which could be inferred from orientation toward the window was that variety present in all binocular vision. The other methods employed by TORELLE are not thus open to criticism, and her conclusions are well established. She, as well as PARKER, finds that orientation to light frequently takes place without locomotion. If one eye be covered the animal orients obliquely to the light when at rest. In spite of this fact it goes directly toward the light as did *Ranatra* when so blinded. When an individual is put in direct sunlight it will do one of two things. If there is a possibility of its walking into the shadow without losing its orientation to the sun it is likely to do so, but frequently it varies the process by hopping into the shadow and then turning around so as to come to rest with its head toward the light. The field toward which the animal will orient for the time being is thus chosen in the same manner as COLE describes for certain insects. Some features of the frog's response are more mechanical than those we have just been considering. While sitting facing the light it may be made to raise or depress its head in an effort to keep its alignment with the rays if their angle of incidence upon it be changed. The behavior of the animal at low temperatures is probably related to its hibernating habit. Below 10° C. in air it becomes negatively photo-

tactic and crouches down making feeling motions with its head. A very similar condition obtains when it is in water.

THE REVERSAL OF PHOTOTROPISM BY MEANS OF CHEMICALS.

A few scattered cases have been known where some substance in solution has changed the light response of an aquatic animal supposedly through its chemical effect. LOEB ('06) alone has attempted a duplication of this process experimentally. He has succeeded in making a number of organisms positive by adding a trace of acid to the water containing them. Fresh water Copepods, *Daphnia*, *Gammarus*, and *Balanus* larvæ, as well as *Volvox*, have been made positive in this way. LOEB thinks it probable that the hydrogen ion is the active factor, because normal salts of effective acids produce no change. Alkalies affect the phototropism by destroying the activity of the acid. *Volvox* differs from the crustaceans in its behavior toward alkalies in that they act directly upon it to make it positive. Hydrochloric, oxalic, and acetic acids reverse, but less quickly, than carbon dioxide. Low temperature has the same effect as acid upon most of the animals mentioned. It may also be made to reinforce the effect of acid.

A hypothetical substance within the animals which is affected by the temperature and chemical condition of the water is invoked by LOEB to explain these reversals. His theory is also extended to cover changes due to temporary physiological states, as for instance the reversal of the *Porthesia* larva upon becoming well fed. He argues that acid can not favor the production of a chemical compound producing a positive condition because less acid is required to produce the positive state at 10° C. than at 20° while the velocity of a chemical reaction is more rapid at the higher than at the lower temperature. Therefore a substance favoring negative reaction is built up by the protoplasm and its formation or activity is hindered by acid. Or possibly a compound favoring positive reaction and situated in the body may have its activity checked by a different one in the retina. Acids by hindering the formation of this last would produce positive phototropism. An increase in temperature would augment the velocity of its formation and so produce negative response. LOEB did not mention that a rise in temperature makes some animals positive; this fact makes necessary a more general form of the theory.

MAST ('07) in his paper on *Volvox* makes use of the principle of reversible chemical reactions in much the same way as LOEB. He further takes into consideration the significance of the substances on the opposite sides of the equation and recognizes that any theory must explain reversal in either direction for each kind of stimulus affecting the light reaction. He has especially in mind the reversal due to change of light intensity but applies it to other kinds as well. His reasoning is as follows for the case in which great intensity changes the usual positive reaction to negative. Let X stand for a substance, on the one side of the equation and Y for one upon the other. Suppose an increase of X beyond a definite amount to produce a positive reaction and of Y a negative one. When X and Y are equal the animal is neutral. Since change of temperature produces a new equilibrium in any reversible chemical reaction, thus altering the relative amounts of the substances on opposite sides of the equation, it is reasonable to suppose that light changes can do the same, inasmuch as they also affect the amount of energy involved. If we suppose intense light to fall upon an animal in which the substances are of the proportion $X = Y$

we would soon get a decrease of X and an increase of Y . The equation would read $X - = Y +$. Y being increased from the amount giving neutrality the animal is made negative. A reversal of this process would occur in sufficiently weak light. Acclimatization of the animal consists in changing the proportions of X and Y which give the neutral reaction.

The correlation by LOEB and MAST of reversal of light response and reversal of chemical reaction is suggestive and tempting. Unfortunately it is difficult to test its validity by experiment. Also, while it is beyond question that light may cause chemical change it is doubtful whether it can produce a reversal of reaction.

A considerable number of agencies have been referred to by which reversal may be brought about. Among them may be named heat, mechanical and chemical stimuli, the various tropisms, condition of development of the individual, temporary physiological states, such as hunger and sexual activity, previous stimuli, and certain stereotyped procedures. Inasmuch as two fairly definite types of light response have by this time become distinguished, there is encouragement to study the effect upon them of the various agencies which have just been named. LOEB and some others have already given a certain amount of attention in this direction. It is one of the tasks which lie next at hand in the comparative psychology of lower animals.

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LITERARY NOTICES.

Pfungst, Oskar. *Das Pferd des Herrn von Osten (Der kluge Hans). Ein Beitrag zur experimentellen Tier- und Menschen-Psychologie mit einer Einleitung von Prof. Dr. C. Stumpf sowie einer Abbildung und fünfzehn Figuren.* Pp. 193. *Leipzig: Verlag von Ambrosius Barth.* 1907.

Clever Hans has been in the public eye for four or five years and many charming magazine stories have been written about his wonderful and supermundane powers. Hans and his master, Herr VON OSTEN, apparently were first brought to scientific and world-wide popular notice by the zoölogist, SCHILLINGS. So wonderful were the attainments of the horse that a "Hans commission" of thirteen men was chosen from widely different scientific fields and asked to solve the question as to whether there was any secret means of rapport between horse and master. The commission reported that Herr VON OSTEN did not, at least consciously, control the responses of the animal by means of signals.

STUMPF's investigations of the behavior of Hans began on the thirteenth of October and were continued until November 29, 1904. Herr O. PFUNGST and Dr. E. v. HORNBOSTEL were present during these observations. The main conclusion reached was to the effect that visual signs of one kind or another were utilized by the horse in making the proper responses.

O. PFUNGST then continued the work in two ways. First, he made a thorough test of the various acts of Hans, then determined the sensory cues to which the horse reacted: Second, he substituted human subjects for Hans, who were required to answer questions (similar to those put to Hans) by utilizing the same kind of data which Hans employed.

The experimental work was conducted partly in an open court and partly in a large, white tent. Carrots, sugar and bread were the rewards for correct answers. All questions asked were put in such a form that the answers could be given by tapping a certain number of times with the foot.

1. Can Hans read numbers? Printed or written numbers were placed on cards and exhibited to Hans. Hans was supposed to tap the appropriate number of times. Two methods were tried. First, the questioner himself was ignorant of the number displayed; second, the questioner knew the correct answer. When the questioner was ignorant of the answer, only 8 per cent of correct responses was returned. On the other hand, when the questioner knew the answer, 98 per cent of correct answers was returned.

2. Can Hans read words? Such words as "Hans," "Stall," etc., were printed on placards and arranged in a numbered series on a board. The horse was asked to indicate by tapping on which placard any chosen word lay. When the word chosen was unknown to the experimenter, no correct answers were returned, when known to the experimenter, 100 per cent of correct answers was given.

3. Can Hans spell? The letters of the alphabet were arranged in horizontal rows on a board. Hans had to indicate first the row, and then the position in the row, of each letter called for in the word. The experimenter did not know the positions of any of the letters of the alphabet except *s* and *a* (the positions of these were purposely ascertained). Hans was asked to spell such words as "Schirm," "Arm," "Rom" and "Hans." Under these conditions, Hans was a complete failure. Afterwards, when the questioner knew the positions of all the letters, the horse not only could "spell," but also could answer questions involving several long words.

4. Can Hans make arithmetical calculations? The method adopted in this test was as follows: Herr von OSTEN would whisper a number into the ear of the horse which was unknown to the rest of the observers. PFUNGST would then give another number in the same way and then the horse was asked to add the two numbers. The answer, of course, was unknown to all. In 31 tests of the above type, the horse returned correct answers in three cases. In 31 cases where the questioner knew the answer, 29 correct responses were made.

5. Can Hans even count? The Russian kindergarten counting device (abacus) was used in this experiment. First, the questioner turned his back upon the machine and then shoved forward a certain number of balls. (The questioner in no case knew the number of balls which he had actually pushed forward.) The horse was then asked to indicate the number of balls which had been advanced. No correct answers were given. On the other hand when the questioner knew the answer, Hans in all cases responded correctly.

6. Memory tests. In the absence of the experimenter, a number, or the day of the week, was mentioned to the horse which he was to indicate to the experimenter when the latter returned. In ten trials, only two correct answers were returned. One of the two correct answers was the number three which Hans always "played" when in doubt.

7. Musical memory. A little one octave harmonica was operated in an adjoining room. Hans was asked to indicate whether the first, second, or third, etc., tone had been played. When not attended by the experimenter, the horse always failed. When the questioner could be observed by the horse, all the answers were correct.

In summarizing the results of these experiments, we find that when the questioner knew the answer to the proposed query, from 90 to 100 per cent of the horse's responses were correct. On the other hand, when the answer was unknown to the questioner, the highest percentage of correct answers was 10. According to the author, these latter correct answers must be ascribed to accidents. PFUNGST concludes "that Hans can neither read, count nor perform calculations with numbers. He can distinguish neither coins nor cards. He is not acquainted with the calendar nor with our system of time. He cannot even recall a number given him but a moment before. Finally, there is no trace of a musical ear. From all this, we must conclude that the horse is unable to work independently, but is dependent upon his environment for particular stimulations" (free translation).

After the above data had been obtained, the author tested very carefully the means by which Hans gets his cue. Without going into detail in this part of the work, it may be said at once that if visual stimulation were cut off by means of blinders (the horse has a wonderfully wide field of vision) the horse could no longer give the correct responses. In making his responses, it was observed that Hans never looked at the objects to which he was supposed to react, but always at his questioner.

The sensory stimulations from which Hans took his cue consisted of *certain slight movements of his questioner's body*. After Herr VON OSTEN had stated the problem, he tended always to *bend the head and trunk slightly forward*; whereupon Hans extended his right foot and began to tap without putting his foot back after each successive tap. When the desired number of taps was reached, Herr VON OSTEN would give a *slight upward jerk of the head*. At this second signal, the horse would retract the foot to its normal position (this last movement was never counted). Now when the horse had ceased to tap, the questioner would raise the head and trunk to an upright position. This second and more extensive movement (that is, more extensive than the slight upward jerk of the head) cannot be regarded as the signal for the retraction of the foot. If the larger movement, however, did not follow the slight upward jerk of the head, the horse would give a single vigorous tap with the *left* foot, without however first extending it. Horizontal movements were without effect in eliciting responses from Hans. All downward motions of the body, eyebrows, nostrils, arms, etc., were signs to begin the tapping movement, whereas the raising of these parts was a signal to cease tapping.

The results of the experiments conducted in the laboratory upon human subjects in the rôle of Hans form an interesting contribution to the study of the psychology of involuntary movements.

Surely, this careful and painstaking work of PFUNGST may be prescribed as an antidote henceforth and forever to those untrained but enthusiastic observers who may be filled with the desire to describe the doings of pet animals in glowing anthropomorphic terms.

J. B. W.

Yale Psychological Studies. Edited by CHARLES H. JUDD, n. s. vol. 1, no. 2. *Psychological Review Monograph Supplements*, vol. 8, no. 3, pp. 227-423. 1907.

The second half of the first volume of the new Yale Studies contains five papers, at least four of which show that perfection of experimental technique which is characteristic of Professor JUDD's laboratory. In Tonal Reactions, Dr. E. H. CAMERON gives an interesting study of tones as produced by the human voice, both with and without distractions. "The attempt to sing a uniformly sustained tone is not successful. The beginning of the tone is markedly irregular and there is a tendency to raise the pitch towards the end of the tone. There is usually a harmonious relation between the sung tone and the distracting tone." Mr. F. N. FREEMAN contributes some Preliminary Experiments on Writing Reactions which connect interestingly with the Analysis of Reaction Movements contained in the first half of the volume. Both of these papers have important bearings on the mechanism of consciousness, of which the full significance, in the reviewer's opinion, will appear only later. Mr. H. N. LOOMIS reports on Reactions to Equal Weights of Unequal Size. He finds that the weight of smaller size is usually raised later than the larger weight, and that the hand which lifts this latter has a much greater muscular tension. With practice the illusion tends to disappear, and so too these differences in the manner of lifting. In Studies in Perceptual Development Professors JUDD and D. J. COWLING describe experiments in which subjects learned to draw complex figures. Each figure was shown repeatedly for ten seconds, and after each view the subject reproduced once as well as he could what he had seen. The issue concludes with some remarkable Photographic Records of Convergence and Divergence, including a theoretical discussion of the mechanism of perceptual

unity, by Professor JUDD. In general, lateral movements of both eyes in the same direction are a more thoroughly established form of coördination than are movements of convergence and divergence; but many particular facts of movement are brought out which are well worth studying in detail. As is well known, the author denies the significance ordinarily attributed to sensations of movement in the formation of spatial and other percepts, and his view is expressed in the very pregnant and, in the reviewer's opinion, just proposition: "The only concept which is of any value in the clear explanation of perceptual unity is the concept of coördination," i. e., the coördination of motor response.

E. B. H.

The Archives of Psychology. Edited by R. S. WOODWORTH. *New York, The Science Press.*

The *Archives of Psychology* is a continuation of the psychological part of the *Archives of Philosophy, Psychology, and Scientific Methods*, of which one volume, consisting of the following monographs, was published.

Measurements of Twins. By EDWARD L. THORNDIKE.

Avenarius and the Standpoint of Pure Experience. By WENDELL T. BUSH.

The Psychology of Association. By FELIX ARNOLD.

The Psychology of Reading. By WALTER FENNO DEARBORN.

The Measurement of Variable Quantities. By FRANZ BOAS.

Linguistic Lapses. By FREDERIC LYMAN WELLS.

The Diurnal Course of Efficiency. By HOWARD D. MARSH.

The Time of Perception as a Measure of Differences in Sensations.

By VIVIAN ALLEN CHARLES HENMON.

Below we give review notices of the numbers of the *Archives of Psychology* which have appeared.

Norsworthy, Naomi. The Psychology of Mentally Deficient Children. *Archives of Psychology*, no. 1, pp. iii + 111. \$1.00. 1906.

The author presents the results of an experimental study of groups of defective children, and discusses the scientific and practical significance of the facts which she has discovered. She briefly summarizes what little experimental work had been done in this field, previous to her own investigation, and insists upon the need of the exact measurement of a number of the important characteristics of normal and defective children.

"I have sought to determine," she writes, "(1) whether the mental defects of idiots are equaled by the bodily, (2) whether idiots form a separate species or not, and (3) whether the entire mental growth is retarded, that is, whether there is a lack of mental capacity all around." In order to get data for the solution of these problems she made measurements of the following traits. Mental Traits: Efficiency of perception; memory of unrelated ideas; ability in the formation of abstract ideas; ability to appreciate relationships and to control associations; perception of weight; and motor control. Physical Traits: Height; weight; pulse and temperature.

The measurements which were made led the author to conclude: (1) That there is a decided difference between bodily and mental deficiency (p. 69); (2) that idiots seem not to form a special class or species, at least as far as intellectual traits are concerned, but that they are included as part of a large distribution (p. 77); and (3) that there is not among idiots an equal lack of mental capacity in all lines (p. 82).

Of special interest to educators, and to others who are interested primarily in

applications, is the discussion of the education of defectives. It is the author's belief that the difference between the defective and the normal child is one of degree and not of kind, and that for this reason the educational methods applied to the former should not differ in principle from those which are used for the latter.

R. M. Y.

Franz, Shepherd Ivory. On the Functions of the Cerebrum: The Frontal Lobes. *Archives of Psychology*, no. 2, pp. 64. 50c. 1907.

This monograph is one of a projected series on the functions of the cerebrum, particularly on those of the so-called association areas. The first section (pp. 5-11) is introductory and historical; the second (pp. 12-28) summarizes and criticises previous studies on the frontal lobes; the third (pp. 29-34) gives the author's methods and the fourth (pp. 35-62) his results.

In criticising previous results the author concurs with others in giving slight weight to MUNK's statement that dogs show motor disturbances of the trunk muscles after extirpation of the frontal lobes. He noticed no such disturbances, at any rate, in the cats and monkeys on which he operated. Nor do his experiments lend any support to FERRIER's conclusion from experiments on monkeys (confirmed in part by GRÜNBAUM and SHERRINGTON for the chimpanzee) that "frontal centers are concerned with the movements of the head and eyes" (p. 14). A somewhat detailed review of the evidence adduced by many to show that the frontal lobes are the centers of inhibition, attention or of higher mental processes leaves the impression that this evidence is either inconclusive or is actually opposed to these inferences. His general criticism of such work is that the observations are too casual and that the accounts show too clearly the lack of "a careful analysis of the mental condition" (p. 24) to be taken as univocal proof.

FRANZ attempts, in his own experiments, neither primarily to discover possible motor centers nor a connection between the frontal lobes and so-called higher mental processes, but "to determine whether or not animals with frontal lobe destruction retained simple associations or could form associations" (p. 30). The animal (a cat or a monkey) was placed in a box from which, by pulling a string or turning a button, it could escape and obtain food. For monkeys an intricate "hurdle" was sometimes used. The habit was thoroughly formed while the animal was still in a normal condition and its retention tested after the lapse of some weeks or after severance of the frontal lobes, which were left in situ, from the rest of the cerebrum. In some cases the operation was first performed and then the attempt made to form the habit. "If the time for the performance of the act of turning the button or pulling the string, etc. (after the operation), remained the same as when the earlier experiments were made, we are warranted in saying that the association is retained and the nervous connections for the performance of the habit have not, in the case of extirpation, been interfered with" (p. 34). In cats, the attempt was made to extirpate always in front of the crucial sulcus and often the section was made in the immediate neighborhood of the supraorbital fissure. For monkeys the endeavor was to limit the lesions to that portion of the cerebrum anterior to the precentral fissure. From neither of these extirpated regions did stimulation give any constant motor response. After the formation of the habit, but before the operation, the animals were put away for a week or more with no practice, when their retention of the habit was again tested.

The results on four cats are first reported, all of which were practiced until they could release themselves from the box in from 1 to 6 seconds. Both frontals were then removed. During periods varying from seven to fourteen days after the operation these animals were tested and were found to have lost the habits that they had formed. In these, and in the other cases as well, two minutes were given the animal in which to open the box. On ten monkeys the same operation (severance of both frontals), after the required habit had been formed, resulted in the loss of the habit by six of the animals and its retention by four, although the time of performance, in the latter cases, was somewhat longer than before the operation.

As the result of the experiments designed to test the ability of the animals to learn a habit for the first time after the operation (on both frontals) had been performed, or to relearn it after it had once been lost as a result of the operation, it was found that two cats easily acquired the box habit after both frontals had been severed from the rest of the cerebrum and that two of the cats and two of the monkeys could relearn the habit lost after operation. In the case of one of the cats that learned the habit after operation the author remarks that "the curve of learning in this animal was about the same as that in an animal before the removal of the frontals" (p. 57).

That the loss of newly acquired habits after the removal of the frontal lobes, which is the more frequent result in these experiments, is not due to surgical shock and does not result after the removal of other parts of the cerebrum is shown by the cases in which habits were retained even after the frontal lobes had been severed and by others in which the parietal lobes were removed without detriment.

The inference that the author draws from his results and from those of other investigators is that "the frontal lobes are concerned in normal and daily associational processes and that through them we are enabled to form habits and, in general, to learn" (p. 64). Four cases were mentioned, however, in which the formed habit was retained after cutting away both frontals, two in which the habit was learned for the first time after the operation and four in which it was relearned. The author suggests, in explanation, since the learning period, in those cases in which the habit was retained even after operation, was longer than in other cases, that it had become a reflex and was therefore due to the functioning of the lower centers, identifying these cases with others in which he observed that habits of long standing, such as coming on call or jumping on the experimenter's shoulder, were also retained after the operation. The instances of learning and of relearning, after the removal of the frontal lobes, he supposes to have been due to the activity of the still uninjured parts of the cerebrum, in particular of the remnants of the frontal lobes still left intact after operation. Both suggestions are interesting but, as the author himself feels, further and more crucial experiments are needed to define the exact difference between a *new* habit (not retained after operation) and an *old* habit (retained). It is unfortunate, in this connection, that no exact record is given of the length of the whole training period for each animal, of the intervals between tests and of the number of trials at each test. YERKES¹ has recently shown the importance of such records in determining the efficacy of training. Further, if those portions of the frontal lobes which were severed from the rest of the brain are *normally* concerned in the formation of habits, ought habits to be learned

¹ YERKES, R. M. *The Dancing Mouse*. New York. 1907.

as quickly (as one case, at least, indicates) by the parts still left intact after the operation? In short, before the general inference from the experiments can be looked on as more than highly probable, further investigation and more exhaustive records, of the kind just indicated, are much to be desired. FRANZ himself intends to experiment further.

ROSSELL P. ANGIER.

Thorndike, Edward L. Empirical Studies in the Theory of Measurement. *Archives of Psychology*, no. 3, pp. 45. 50c. 1907.

A discussion of statistical methods, in the light of the author's experience. Measurements of type and variability, and measurements of relationships are considered with a view to convenience, economy, and directness as well as to precision.

Lapisky, Abram. Rhythm as a Distinguishing Characteristic of Prose Style. *Archives of Psychology*, no. 4, Pp. iii+44. 50c. 1907.

Ruediger, W. C. The Field of Distinct Vision, with Special Reference to Individual Differences and their Correlations. *Archives of Psychology*, no. 4, pp. 68. 1907.

The author mapped out the field of acute vision in eighteen subjects, with a view to finding "characteristic individual differences" and to ascertaining whether the size of this field is correlated with "reading rate, the color zones, visual acuity, retinal inertia, and other phenomena of vision." The field of acute vision is defined as the area within which the letters *n* and *u* (of a certain font of type) are discriminated 75 (and again 90) per cent of the cases, when exposed for a fixed length of time (less than the reaction-time of the eye).

The shape of this field is found to vary "in different individuals from a 'square-oval,' about twice as long horizontally as wide vertically, to a circle;" and "the size of the field varies approximately as 2-1 in the horizontal diameter, as 1.5-1 in the vertical diameter, and as 2-1 in area." There is some correlation between the size of this field and the acuteness of vision itself, which amounts, if the latter is determined by GALTON's test, to nearly +.69 (PEARSON coefficient). In this correlation not eighteen but twelve subjects are used, and this value of the coefficient should not be further employed without a careful reading of the author's text (pp. 46-49). "There is little or no correlation between the horizontal extent of distinct vision and the 'A' test, the number of lines that can be seen simultaneously, reading rate, and the number of pauses per line. Reading rate apparently does not correlate with any of the attributes of vision, but it correlates highly with the smallness of the number of reading pauses per line."

A simple method of Professor WOODWORTH's is described, for measuring correlation (pp. 37-39). It can be used wherever the individuals compared with regard to a character, can be ranked in ordinal series, and it takes into account this order of the individuals, but not the amounts by which they differ in regard to this character from one another.

E. B. H.

Jones, E. E. The Influence of Bodily Posture on Mental Activities. *Archives of Psychology*, no. 6, pp. 61, 50c. 1907.

The author briefly sums up the chief results of his work as follows: "Pitch is discriminated better (with the body) in the vertical than in the horizontal position;

tactile discrimination is slightly more acute in the horizontal than in the vertical; visual memory is both more rapid and subject to fewer errors in the horizontal than in the vertical position; auditory memory shows the same result as the visual memory; adding can be done more rapidly and with greater precision in the horizontal posture; subjects show greater signs of fatigue in the horizontal than in the vertical posture; a greater number of taps per minute can be made in the vertical than in the horizontal position; and the vertical position is favorable to the strength of grip."

Wells, F. L. A Statistical Study of Literary Merit with Remarks on Some New Phases of the Method. *Archives of Psychology*, no. 7, pp. 30. 30c. 1907.

Yerkes, Robert M. The Dancing Mouse: A Study in Animal Behavior. *Animal Behavior Series*, vol. 1, pp. xxi + 290. New York: The Macmillan Company. 1907.

It is not putting the matter too strongly to say that Dr. YERKES has in this book given us the most valuable contribution that has yet been made to the study of animal behavior. Having become interested about four years ago in some specimens of the curious Japanese dancing mouse, and finding them readily tamed, easy to care for, and comparatively quick to learn, he undertook a thorough investigation of their sensory equipment and intelligence. The results are stated clearly and concisely in the present volume. Every step in the methods used, every stage in the reasoning processes by which the author's conclusions were reached, is given, so that the book is a real text-book in experimental method.

The dancing mouse, as is well known, gets its name from the fact that when placed in an open space it makes peculiar whirling or circling movements. These movements have been thought to be due to a malformation of the equilibrium apparatus in the ear, and support seems to be given to the theory by the fact that the mice have defective hearing. Yet the statements of various experimenters who have examined the ear are so conflicting that no definite inference can be drawn from them. Dr. YERKES concludes that to explain the peculiar movements of the dancer "the structure of the entire organism will have to be taken into account," and at the same time he finds no "satisfactory ground for considering the dancer as either abnormal or pathological"—an assertion the truth of which would seem to depend upon the meaning assigned to the term "abnormal." To account for the disagreement among different observers of the behavior of the animal, some of whom say that the mouse is markedly deficient in balancing power, while others find no striking defect in this respect, YERKES adopts the suggestion of CYON that there are at least two varieties of the dancing mouse, and has observed evidences of the existence of two different strains among the specimens examined by himself.

The net results of the author's work with some four hundred individuals may be grouped under four heads: those concerning the mouse's power of sense discrimination; those concerning its learning capacity; those bearing on questions of experimental method, and those of interest to students of biogenetics.

1. Three classes of sensory discriminations: auditory, brightness, and color, were investigated. The mice of one of the two lines of descent represented were, with the exception of one litter, throughout their lives insensitive to sounds. Those of the other line showed sensitiveness for a day or two during their third week.

The mice displayed ability, varying with the individual, to discriminate different shades of gray paper, though their capacity in this direction was less than that of a human being. One mouse was subjected to tests of the validity of WEBER's Law, in discriminations of the degree of illumination in different compartments; and the law was found to hold, the proportion $\frac{DR}{R}$ lying between 1-10 and 1-15.

These discriminations were greatly improved by practice.

As regards color discrimination, much of the behavior superficially to be classed under this head appeared on further investigation to be really based on the brightness value of the colors. This value is apparently quite different in the case of the mouse from what it is in the human subject. The red end of the spectrum is much darker to the mouse, being indistinguishable from black and darker than any green or blue. There is some evidence that the mice can discriminate green and red "by some other factor than brightness," but on the whole the problem of their color vision is not solved. The dancer was found to be incapable of distinguishing between two equal illuminated areas of equal brightness but different form. Mice that have learned a labyrinth path are little disturbed in traversing it by being made to do so in darkness, by washing the labyrinth so as to destroy smell clues, or by moving the labyrinth to one side so that the former track is removed. They were a good deal disturbed when the floor was covered with smoked paper, but Dr. YERKES thinks this disturbance was a general one and not the result of loss of a clue. The rôle of the senses of sight, smell, and touch in the learning of a labyrinth path, quite a different problem from the effect of eliminating a sense after the animal has learned the path, was not experimentally tested; observation of the general behavior of the animals led to the conclusion that these senses are all used, but in different degrees by different individuals.

2. The results that bear especially on the mouse's learning capacity are as follows. The dancer is capable of forming habits that involve turning in one direction or another (labyrinth habits), and habits that require in addition visual discrimination, but the former are acquired much more rapidly than the latter. A regular labyrinth, involving turns alternately in two directions, is learned with especial speed. Useless habits occasionally persist for some time, a fact which several other investigators have noted. The mice did not learn by imitating each other. Putting the animals through one of the reactions which they learned, that of climbing a ladder, did aid the learning process. Dr. YERKES's conclusions regarding sex differences in learning capacity are less convincing than his other inferences from results. He says, "In labyrinth tests the female is as much superior to the male as the male is to the female in discrimination tests." Yet in the tables upon which the first part of this statement is based, although the average number of tests which had to be given before the labyrinth was perfectly learned was 18.7 for the males and 13.8 for the females, five of the ten males learned with fewer tests than did five of the females. "Of the five pairs of individuals whose records in white-black training appear in Table 43," says the author, "not one contradicts" the statement that the males are superior to the females in discrimination experiments. This table contains the results of tests of black-white discrimination made at the rate of ten per day; but Dr. YERKES himself points out that the females did better than the males when twenty tests per day were given.

The experiments on the relation of docility to age were not completed. As

regards the persistence of the habits acquired, the white-black discrimination habit, it is concluded, "may persist during an interval of from two to eight weeks of disuse," but "is seldom perfect after more than four weeks." The color discrimination habits never persisted more than two weeks. The white-black discrimination was re-learned, after all traces of it had disappeared, in a shorter time than had been required for its original acquisition, thus suggesting "the existence of two kinds or aspects of organic modification in connection with training; those which constitute the basis of a definite form of motor activity, and those which constitute bases or dispositions for the acquirement of certain types of behavior." As ROUSE found to be the case with the pigeon, experience with one form of labyrinth made the learning of another form easier.

3. The suggestions on method which the book contains are among its most valuable features. In the first place, Dr. YERKES finds that the best motive to employ in studying the learning processes of mammals is not hunger, which is variable in intensity, unfavorable, in its extreme degrees, to the exercise of the animal's full powers, and inhumane; but the punishment of mistakes by slight electric shocks, given through wires on the floor of the discrimination box or labyrinth. So far as my recollection serves, the author first used this method in his experiments on the frog. It has certainly a decided advantage over any method where the motive is constituted by a continuous state in the animal, such as hunger or the desire to escape from confinement. Any continuous state is likely to vary in intensity, and discomfort under confinement is likely to diminish as the animal becomes used to its surroundings. An intermittent stimulus, given when mistakes are made, has a much better chance of producing a constant effect.

Another interesting point in method concerns the evidence which was obtained that apparent color discrimination was really, in some measure at least, brightness discrimination. This evidence consisted in the fact that mice which had been trained to choose a compartment illuminated by green light in preference to one illuminated by red light, on being offered a choice between black and white compartments, chose the white, although before the green-red training they had shown no such preference. Thus it looked as if they had been choosing the green partly, at least, as the lighter of the two visual impressions. This method might well be given a wider scope in the study of the sensory discriminations of animals. It is puzzling, by the way, in view of the evidence that red is much darker to the mouse than to the human observer, to find that a tendency to choose red rather than yellow in tests with colored cards is explained as the result of previous training to go to the brighter compartment in white-black tests.

The results of training tests are throughout stated in terms not of the time required to perform the act, but of either the number of errors made or the number of tests required before the formation of a perfect habit. The time required in traversing a labyrinth, for example, is in the author's opinion a poor index of the perfection of the habit. In this respect his position is the opposite of that taken by WATSON, who states the results of his tests of the white rat wholly in terms of time.

On the whole, the most favorable number of tests per day in the discrimination series, taking into account economy of time and fatigue for both experimenter and animal, was found to be ten.

For labyrinth experiments, the author recommends the use of a standard maze in which "errors by turning to the right, to the left, and by moving forward should

occur with equal frequency and in such order that no particular kind of error occurs repeatedly in succession."

4. Finally, Dr. YERKES made some studies on the phenomena of heredity in the dancing mouse. The subjects of his experiments belonged to two separate lines of descent, which presented certain characteristic differences, the individuals of one line being more like ordinary mice than those of the other line. Observations on several generations indicated a certain inheritance in the latter line of descent of a tendency to whirl to the left in dancing, while those of the former line showed no such tendency. Four generations, a male and a female in each, were tested to see if the training of the parents in white-black discrimination facilitated the learning process in the offspring. The results showed no evidence of the inheritance of this acquired character.

From this superficial survey it will be seen how rich both in result and in suggestion the book is. No less admirable is the spirit in which the work has been carried on; a spirit of scientific conscientiousness, of modesty, and of humane sympathy, untinged with sentimentality, for the animals experimented on. Of comparative psychology, in the sense of an attempt to interpret the mental states of the subjects, there is very little in the book, and that little does not strike one as its most successful feature. For instance, when in labyrinth tests the procedure was adopted of allowing a mouse, as a preliminary, to traverse the maze and escape without getting an electric shock, it is said that this was for the purpose of allowing the animal "to discover that escape from the maze was possible," but there is no discussion of the terms in which such a possibility may have functioned in the mouse's consciousness in subsequent tests, whether as a memory image or merely as an increased tendency to movement. Again, when one method of reaction in the discrimination experiments is designated "choice by comparison," one is left with the interesting problem as to what sort of process the comparison of two stimuli in the mouse's mind may be, and it might perhaps have been better to use a term that would have had a less decided psychic implication. However, if there is but little attempt at interpretation of the mental aspect of the facts observed, the book is almost an ideal example of the kind of work which promises to put comparative psychology on a firm scientific basis.

MARGARET FLOY WASHBURN.

Davis, H. B. The Raccoon: A Study in Animal Intelligence. *American Journal of Psychology*, vol. 18, pp. 447-489. 1907.

This paper describes the habits and instincts observable in adult raccoons in captivity, and it presents the results of experiments to test learning, color perception, and imitation in these animals, together with comparisons of these results with those obtained by other investigators. In this review only the descriptions of experiments and the discussion and interpretation of results will be examined. These may be taken up under the general headings learning, color perception and imitation, and comparisons.

Learning. In the author's experimental study of learning the raccoons were allowed to unfasten the door of a box, reach into it, and get food. Single fastenings, a group of two and a group of three latches, and finally, two combination-locks, each composed of four of the previously learned single fastenings, were used in the

tests. The combination locks demanded that their elements be operated in a fixed order.

We are told that in these experiments each animal at first attacked the box with indiscriminate clawing, but finally settled down to a single habitual method of operating the latch or latches. The formation of this habit was due to "the omission of unnecessary movements and the combination of those required," exactly as described by THORNDIKE in the case of cats. "The steps by which perfection is reached are *very short and blindly taken*"¹ (p. 468). Yet despite this gradualness and blindness of the learning process Mr. DAVIS's adult raccoons showed a "*nearly equal facility*" with monkeys in learning to undo fastenings (p. 487), and their curve of learning follows closely the type of those for the higher animals and *for man* (p. 477).

Mr. DAVIS states, "Experience with former fastenings holds over in the case of new ones leading the animal, at least in certain cases, to begin his attack at the place on the surface of the food-box where he has been accustomed to work. (This has been found by THORNDIKE in the case of cats and denied by COLE in the case of raccoons)." This very important conclusion is based, so far as can be judged from a very obscure statement, on only eight reactions of a single animal. During four of these trials the animal stood on his head and clawed where the latch had been. Presumably the vividness of this experience and COLE's remark concerning an easily discriminated fastening have led Mr. DAVIS to say that such performances are denied in COLE's paper, yet on p. 218 of that paper it is distinctly stated that one of COLE's raccoons clawed twice, another four times *at the side of the door where a latch had been in the preceding test*. Nevertheless COLE's results are characterized as "exceptional." Are we to infer that his animals should have clawed eight times instead of six, or that they ought to have stood on their heads while doing so? Notwithstanding the tremendous weight given by Mr. DAVIS to this performance of a single individual, we are told that the raccoons seemed to reach a sort of "generalized manner of procedure" which enabled them to deal more promptly with any new fastening. This half-subjective, half-objective term, "generalized procedure" is vague in the extreme. Does it mean, as pointed out by COLE (p. 218) that "in future new boxes the animals seemed to pick out the new latch and work directly at that as if experience led them to attack movable objects within the box, or else objects which gave a click or other sound when operated?" COLE continues: "These facts, with others to be mentioned, indicate, I think, that the raccoon's learning to operate a latch includes something more than a mere mechanical coupling up of a certain instinctive act with a given situation." KINNAMAN (p. 122) says more boldly, "It looks very much like the possession of a general notion fairly well represented by projecting-thing-has-something-to-do-with-it, and so they attacked the projecting thing and not something else." If the conclusion as to "generalized procedure" does mean this, it seems to contradict point blank the conclusion based on the special procedure of the single animal which clawed eight times at the side of the door where a bolt had been in the preceding test. Probably THORNDIKE would be first to protest against confirmation by the exceptional behavior, super- or sub-normal of a single animal, when this behavior was contradicted by other records.

¹ Italics are the reviewer's.

According to the author, "Perception of the essential relations, if present at all, is dull and stupid in the last degree" (p. 468). Yet "there is an evident ability to respond to *small differences in complex relations*. How far the perception of such relations really enters is, however, at present in doubt" (p. 477). Practical denial is weakened to doubt within a few pages, because of the contrast between what one raccoon did and what they all did. However, the study of the perception of *relations* in animals is a new field. It is enough for most workers at present if they can *prove* the perception of an easily discriminated object and say with certainty whether it is a visual, olfactory, or tactile perception. Perhaps, however, Mr. DAVIS means that the raccoons did not perceive the fastenings, though they responded to small differences in them, for his confirmation of THORNDIKE commits him to the latter's statement (p. 80) that "the loop is to the cat what the ocean is to a man when thrown into it, when half asleep."

This apparent conflict between conclusions is evident throughout the paper and it seems to be due to the old discrepancy between isolated observations and the final and impersonal result of systematic records, a conflict which THORNDIKE tried hard to terminate.

In working the combination locks the animals learned "order" and "amount of effort" at somewhat different rates. "The table seems to show that the memory of the order is more readily perfected than that of the muscular adjustment required for each particular locking device" (p. 469). Does this mean two types of "memory," as is indicated by this quotation, or merely two rates of habit forming, or a type of memory and a case of habit forming, which we should expect to develop at two different rates? Varying the locking devices would doubtless have explained the phenomenon or analyzed it for us. If it is due to mere defect in method, varying the device would have eliminated it. So the observation seems significant for future tests. If we can find two widely divergent rates, we may find a distinction between habit and association. KINNAMAN, who tested monkeys with combinations very similar to those used by Mr. DAVIS, does not call our attention to any difference in the rate of learning "order" and "amount of effort." This adds interest to Mr. DAVIS's observation.

An excellent table is given of the first forty trials of raccoon No. 1 with the single fastenings and groups. The generalized curves are too greatly reduced to be of much value. A curve for KINNAMAN's monkey's is given, but KINNAMAN counted the entire time "no matter whether the monkey was before or behind the box, whether prancing around it or jumping up and down on top of it, so long as he was trying to open it. Some of these efforts were in nowise directed toward the latch" (KINNAMAN, p. 115). DAVIS, on the contrary recorded the time during which the animal was *in contact* with the locking device (DAVIS, p. 465). Surely this difference must be taken into account in valuing his conclusions that the raccoons show a nearly equal facility with KINNAMAN's monkeys in learning to undo fastenings, and that "the monkeys would seem to be a little less clever at the start" (p. 476). COLE had previously concluded that "in the rapidity with which it forms associations the raccoon seems to stand almost midway between the monkey and the cat, as shown by the numerical records for those animals. In the complexity of the associations it is able to form it stands nearer the monkey" (COLE, p. 261). His method of timing agreed with KINNAMAN's and with THORNDIKE's, though his animals were young and exhibited "play trials." Mr. DAVIS's method of timing

and his failure to mark intermissions in practice precluded the presentation of records of "play trials."

Although Mr. DAVIS finds marked differences in learning due to practice effects, we are nowhere told in what order he used the several fastenings. This is a most serious omission and greatly impairs the value of his paper for comparative purposes. For example, in one case he tested a raccoon on fastening No. 3, then passed to No. 9, and in the latter case finds remarkable stupidity. Now if fastenings No. 9 were really the ninth fastening this animal had tried, the result is new and unusual, but if it is the fourth, third, or second fastening, the animal's behavior agrees closely with that of other raccoons, and entirely loses its marvelous character.

Further, we read that while all the raccoons were "fully grown" when received, yet distinct differences in learning were found between the younger and the older animals. We should expect, therefore, a statement of the approximate age of each animal when received. Instead we are offered what seems to be the most useless possible statement, namely, "the approximate age of each animal" *at death or escape or for the summer of 1907*, some months after his work was completed (cf. pp. 462, 448). This defect greatly lessens the value of the experimental records. Fortunately reparation can be made by the publication of the date at which each animal was received, the length of time during which it was tested, and the order in which the tests were given. This addendum ought certainly to appear.

Finally, so far as we can learn from the paper, only one box was used and the latches were all so fastened to it as to be most inconspicuous. This, of course, tends to stamp in the box feature of the situation, and, therefore to make the animal more dependent on kinæsthetic sensations. Varying the position and size of boxes and doors gives control experiments which rarely fail to modify an investigator's first conclusions.

The conflict between the author's several conclusions leaves one in doubt whether the raccoons are, in intelligence, nearer the cats, which possibly have "no images or memories at all," or nearer the monkeys which exhibit even "a low form of general notion."

Color Perception. The color perception of the raccoons was tested, and it is concluded that they do not discriminate colors as such, but depend on differences in brightness alone for their successful reactions. While the tables seem to show this they may prove merely that discrimination of brightness is easier for the animals to make than discrimination of color, for the method employed is very defective.

With the first piece of apparatus used the raccoons could both look into and reach into the vessel which contained the food, and into the five similar vessels which were empty. The experimenter must have felt this disadvantage, for the second piece of apparatus "*did not allow the animal to look into the container in which the food was placed*" (p. 479), but the food could be obtained by reaching through an opening 2 by $1\frac{1}{2}$ inches, in the vertical slides. The food was placed back of one color and when this was moved every other color was given a new position also. Thus with the second device each container could be explored by touch. If the animal reached into a no-food vessel an error of color discrimination was recorded against him. There seems thus no means of distinguishing true errors of color discrimination from the cases in which the animal paid no attention to the colors, except that brightness tests gave better results than color tests. "The two pieces of apparatus were used indifferently." Under these conditions there were 52 per cent

of right choices in brightness tests, and 24 per cent in color tests. One of the four animals made 40.7 per cent of right choices in the color tests. This fact is ascribed to brightness differences in the colors used. It must be remembered that by chance alone the animals would have made 17 per cent of right colors. It seems possible, therefore, that both averages are too low, due to the steady pressure of an instinctive impulse, for the reviewer has used the first piece of apparatus and found that *apparently the raccoons could not pass a single food container without both reaching into it and looking into it*. Instead, the animal would go to one end of the row of vessels, explore the first one carefully both by touch and sight, then the next, and so on until the vessel with food in it was found; then it would go on in the same way to the end of the row, and back again, rarely skipping a single vessel. The raccoon has, then, a very strong instinctive impulse to reach into and to look into all sorts of openings.

Imitation. No certain cases of imitation were discovered by the author.

Comparisons. Mr. DAVIS "correlates" his results with those of BERRY on the white rat and of COLE on the raccoon. BERRY very properly compares the behavior of a rat which learns by trial and error with one given an opportunity to learn by imitation and concludes, "It seems to me that we ought to be able to say *a priori*, in the light of these facts, that no ordinary rat would be able to open a door by pulling a string, simply from having seen another do it, without first making a number of random movements." To this Mr. DAVIS replies, "It is upon such a slender basis that Mr. BERRY infers imitation" (DAVIS, p. 483). This seems quite unfair. It is upon no such basis that BERRY infers imitation, but upon repeated experiments in which the imitator developed a tendency (not present before) to pull a knot after seeing another rat pull it many times. On such experiments as a "basis" with most carefully arranged control tests, which proved that the tendency was due to example alone, Mr. BERRY makes the very conservative observation quoted, and first rate confirmation of its truth has been forthcoming. WATSON has demonstrated the immense rôle that kinæsthetic sensations play in the life of the rat, and BERRY has found an advance upon this grade of imitation in other animals. Why invert BERRY's argument to the neglect of his recorded facts?

So BERRY is said to "beg the whole question" because he "lays great stress on the visual sensation as the chief factor in what he calls the final imitative act." Here again it would seem as if BERRY were, instead only allowing proper importance to kinæsthetic sensations, since the rat which learns by trial and error has them, while the imitator must depend first of all on sight. The reviewer is unfamiliar with the behavior of rats, but he can say of raccoons that the experimenter had better lay *very great stress* on their visual sensations of movements for they are almost as skillful muscle readers as the trained dog, "Roger," of recent fame. The danger is that the experimenter will not ascertain until too late how delicate are the movements which the animals can detect by sight.

In a second correlation, what COLE described as due either to imitation or to the presence of visual images in raccoons has, what seems to Mr. DAVIS, a third explanation. As this additional explanation offered is based on a complete misunderstanding of the conditions of the experiment we may pass it by with the remark that perhaps COLE was not clear in his description.

A third correlation with COLE's work, and one already referred to, is of so vital importance in interpreting the behavior of raccoons that all the relevant statements

must here be brought together. (1) THORNDIKE (p. 80) is authority for the statement that "cats would claw at the loop or button when the door was open," and "at the place where the loop has been though none was there." (2) COLE, pp. 218, 253 found that raccoons did neither of these things, though they were given opportunities to do both. (3) When the latch is fastened to the side of the box and on the opposite side of the door from that of the immediately preceding test the raccoons did claw a few times (COLE records six times by two young animals, in their earlier trials; DAVIS, apparently, eight times, one adult animal, whether earlier or later trials is not stated) at the place where the latch had been. If Mr. DAVIS had used an easily discriminated fastening like a loop or platform his results would have been more easily comparable with THORNDIKE's and COLE's. He does not say that the raccoon ever clawed at a fastening when the door was open. Surely we must not expect the raccoon, in his early trials, to limit his efforts to projecting objects as he will do in his later trials. Do Mr. DAVIS's records, then, really agree with THORNDIKE's statement that "the loop is to the cat what the ocean is to a man when thrown into it when half asleep" (THORNDIKE, p. 80)? This is a phrase meant to describe about as near a total lack of discrimination as "thought can pump out of itself." Is it consistent with the raccoon's responding to small differences in complex relations? Truly the small number of cases must be recorded, but they must not be overloaded with conclusions.

It is, indeed, an ungracious task to find defects in another's work and in a previous résumé the reviewer largely refrained from it. Yet the first step in assigning the true value to the record of an investigation is to compare interpretations in the same paper. From such comparisons emerges a truth, well known to most investigators. In our early experiments with an animal his behavior suggests ambiguous or contradictory conclusions. This is a hint from the animal that our apparatus or method or both need modification. Watch the animal closely and the direction the modification should take will be suggested. Refuse to modify the method or cling to apparatus already used with some other animal and you remain in the first stages of your work with contradictory or doubtful conclusions on every side. Care in varying the conditions seems to show, however, fairly consistent behavior in any one type of animal.

Finally it appears that cats and monkeys are so widely different in intelligence that it is very difficult to interpret the behavior of raccoons as agreeing with that of both the other animals.

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